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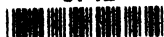
BY

A. G. TANSLEY

VOLUME VI

WITH SIX PLATES AND NUMEROUS FIGURES
IN THE TEXT

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THE DISTRIBUTION OF *NARDUS STRICTA*
IN RELATION TO PEATBY WILLIAM G. SMITH¹

(With Plates I and II and a Vegetation Map)

*Nardus stricta*² is a widely distributed grass on moor and heath, and it becomes a dominant or co-dominant species in plant associations which on preliminary examination seem to have little relationship. This distribution has not tended to a clear concept in our literature of the position of *Nardus* associations. In Switzerland the distribution of *Nardus* has been frequently recorded by Stebler, Schröter, and others, with much the same result. Thus Brockmann-Jerosch (2) in summarising the *Nardus stricta* type points out that this abundant grass occurs in associations so varied that it is difficult to say anything comprehensive as to its habitat, and still more difficult to characterise the common features of the habitat. It occurs on dry, sandy, non-humous, porous morainic detritus, on *Sphagnum* cushions on the "hoch-moor," on dry humous hummocks amongst the grazing lands, and on raw humus in open woods passing over into *Vaccinietum*. The habitats range from those apparently dry or physiologically dry, to others which are usually described as moist; the substratum varies from pure humus to soils without humus.

This contribution presents our observations on the distribution of *Nardus* as a characteristic plant in a zone which follows the margin of peat moors in northern Britain. It was charted by Mr Macpherson as an almost continuous zone surrounding the upland peat plateau of the Moorfoot Hills in Peeblesshire, and in adjoining counties. The zone is so constant that it is represented on almost every "six-inch" Ordnance Survey sheet (1:10560) over this area of 120 square miles of south-east Scotland. We also know that there is an

¹ The original intention was to publish this as a joint contribution along with Donald Macpherson, B.Sc., who for nearly three years was field assistant in an Agricultural Survey promoted by the Development Commission through the Edinburgh and East of Scotland College of Agriculture. Mr Macpherson obtained a commission in the R.F.A., was wounded in France on September 26th, 1917, and died in hospital on November 10th. The manuscript was prepared in the hope that he might be able to revise it, but this was not to be. The significance of the distribution of *Nardus* was first perceived when we were in the field together in September, 1913, and Mr Macpherson included it in his programme. He prepared the field maps for the area and summarised his observations in a carefully kept daily log, which has been available for reference. The *Nardetum* was discussed from time to time, and I believe that this contribution represents Mr Macpherson's views, although it is probable that he could have added to the details from memory.

W. G. S.

² The popular names include bent, white grass, mat grass, mat-weed, wire-grass, and nard.

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extensive occurrence of the same zone of Nardetum in other parts of Scotland and in the Pennines of northern England. It is further indicated more or less definitely in various other areas described by home and foreign authors.

NARDETUM MARGINAL TO PEAT.

Nardus grassland is an important type of vegetation when considered from the point of view of stock-grazing. In itself it is one of the less valuable types of herbage, hence the necessity for observing its relation to other types—on the one hand its evolution, on the other its displacement by herbage of greater value. *Nardus* has therefore been charted in southern Scotland as part of a survey primarily intended to show the distribution of better and inferior types of herbage available for grazing. At first there was difficulty in defining the association because of the variation in the frequency of such plants as heather (*Calluna vulgaris*), blaeberry (*Vaccinium myrtillus*), purple moor or blow grass (*Molinia*), dwarf rush (*Juncus squarrosus*), and two combinations of grassy herbage. After a sufficient number of records were obtained it became evident that there was a plant association characterised by dominance of *Nardus stricta* which resolved itself into a Nardetum zone marginal to areas occupied by peat and its vegetation, also that the distribution was determined largely by that of peat (Fig. 1).

This is a facies of the Nardetum widely distributed in the lower sub-alpine hill groups of northern Britain, and we have found the concept of great value in orientating the distribution of *Nardus*. Whether all grassland characterised by *Nardus* can be grouped into this facies is still an open question. There is reason to believe that the Nardetum may arise away from the influence of peat, on poor leached soils, both those recently eroded and those recently deposited, but for the present these are not further considered.

Some observations bearing on this facies of the Nardetum are included in notes on the "Grass Moor Association," in *Types of British Vegetation* (15, p. 282). This association is also indicated in the earlier memoirs on British vegetation by F. J. Lewis, M. Hardy, R. and W. G. Smith, etc.¹ The relationship of *Nardus*, *Molinia*, and other grassland species, to peat was more fully demonstrated by C. B. Crampton (3). Later the problem of the vegetation of retrogressive peat has been more fully discussed by C. E. Moss (8, chap. VIII). As to foreign literature, no useful purpose would be served by attempting to summarise the *Nardus* problem, but it may be noted that peat has been recognised as a centre of evolution. Thus Brockmann-Jerosch (2) and Rübel (11) have described alpine fen (Flachmoore) as marginally defined by a zone of *Scirpus caespitosus*, which passes over into a zone of *Carex curvula* and frequently into a second zone of *Nardus*.

Peat which has been little disturbed by drainage or erosion bears plant associations characterised by *Eriophorum* spp., *Scirpus caespitosus*, *Rubus*

¹ For complete list of these, see (15), p. 367.

chamaemorus (on higher plateaux), set in a matrix of cryptogams including mosses¹ and lichens. Partial drainage, underground or surface, is indicated by an increasing abundance of *Juncus squarrosus*, *Calluna*, *Erica tetralix*, *Vaccinium myrtillus*, and *Empetrum*, with lichens and mosses of a more xerophytic type; these occupy the raised hummocks and slopes, while the more endemic moorland associations become restricted to the moister hollows. Where the peat margin is eroded abruptly into cliff-like "peat hags²," there is an abrupt change in the vegetation (Pl. I, Figs. 1 and 2). The plants of the peat margin, generally darker in tone, occupy a slightly elevated tableland above the "hagg," while a few feet lower, below the hagg, the vegetation is grass-like, green, greyish green, or dingy white (according to season), because of the predominance of *Nardus stricta*, frequently mixed with *Juncus squarrosus*, and concealing a lower undergrowth of moorland grasses, etc. (see list). The change from *Eriophorum-Scirpus* to the marginal ericaceous vegetation is generally gradual, that from marginal to Nardetum is sharply defined by the peat hagg.

The evolution of drainage channels in peat has been described by C. B. Crampton (3) and C. E. Moss (8). The peat is undermined by underground water channels formed between the peat and the underlying clay or other substratum. As erosion continues, the upper layers bound together by vegetation are gradually lowered so that the bog becomes undulating with sink-holes, where *Vaccinium myrtillus* takes possession and still maintains an unbroken surface³. More prolonged erosion produces channels which the plant covering can no longer bridge, and a gully with marginal hags appears. Further erosion forms constantly widening open channels generally floored with stones bedded in a mixture of sand, clay and weathered peat. Along the hagged edges the exposed peat constantly "creeps," and is so rapidly eroded that plants can effect no roothold, except here and there a patch of moss, lichen or alga. The peat margin is undercut and blocks of it fall from the higher level to the lower, still bearing growing plants of *Calluna*, *Eriophorum* and others from the peat above. As the hitherto restricted drainage channels approach the outer limits of the peat mass, the hags lie wider and wider apart, and become merged in those hagged margins of the peat which are not directly derived from water channels. The peat area thus becomes defined by a sinuous margin of hags which is generally used in charting areas of peat. The same limit will as a rule be found to define the upper margin of a zone of Nardetum which extends away from the peat for a shorter or longer distance (Pl. II, Fig. 1).

Many peat masses have some part of the margin not defined by hags,

¹ On peat the following have been frequently recorded: *Sphagnum* spp., *Polytrichum commune*, *Aulacomnion palustre*, *Campylopus flexuosus*, *Dicranum scoparium*, and *Hypnum* spp. (D. M.).

² A northern term in common use.

³ This is a common habitat for *Cornus suecica* on northern peat.

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but merging gradually into the adjoining substratum so that the limits of the peat can be defined only roughly by means of a staff. These unbroken margins may be correlated with a gentler slope, although peat hags are by no means limited to steep slopes. Wind is an important factor, and unbroken margins probably result from shelter, although this is not always obvious. Again, the unbroken margin frequently shows indications of greater soil moisture due to underground water which has not found the definite channels so potent in forming the peat hagg. The less abrupt change of substratum has its reflex on the vegetation, so that there is generally a broad transition belt distinguished by an increasing amount of *Nardus*. In the case of a flushed or wet peat margin, *Molinia caerulea* is often the species indicating change from typical peat.

The same transition may be seen in passing from the peat plateau upwards on to a higher knoll or summit. *Nardus* appears as a marginal zone on wasted and redistributed peat. The Nardetum may be continued upwards forming the vegetation cap of the knoll, but, in the case of higher summits this generally gives place to some other type, such as compact dwarf *Vaccinium*, alone or mixed with grasses and lichens, evidently better adapted to the more rigorous summit conditions. There is thus good evidence of the encroachment of *Nardus* on to peat from below and from above. Where the forces which erode the peat continue their action, the upper Nardetum will approach the lower, the peat will become broken up into islands of peat in a mass of *Nardus*, and the final result is a continuous area of Nardetum. The stages in the process can be observed in many areas of retrogressive peat (Pl. II, Fig. 2).

The peat hagg in the moor formation is to some extent comparable to the blow-out in the sand dune formation; in both cases a relatively stable and uniform type of vegetation is broken up and the substratum is redistributed. In the case of peat the chief dynamic agent is underground and surface drainage. When a fissure is formed on a peat surface, the original plant covering is not quickly restored. The fissure becomes a gully, and the evolution of the peat hagg has begun. During winter the peat becomes water-logged, and creeps, thus forming a slimy slope. Outflowing water aids the process of erosion, and the exit of a water channel soon becomes a notch in the peat margin. During spring the surface of the bare peat is dried up and wind erosion begins. Thus throughout the year wind and water are active in breaking down and redistributing the peat. Sheep also tend to shelter under the hags and by rubbing accelerate erosion. Sometimes the breaking up of a peat surface may be catastrophic. The occurrence of a "moss-flow" or "moor-break" (Moorbruch), that is the slipping or movement of a considerable area of water-logged peat, could initiate an extensive system of peat hags¹. This opinion was expressed by P. Graebner (5) on the occasion

¹ The dislocated peat shown in Plate I, Fig. 1, suggests a moss-flow as its origin.

of the International Phytogeographical Excursion (August 1911) to an extensive area of retrogressive peat on the eastern base of Crossfell. If this view holds good for this area there are many other examples in northern Britain.

There is thus much evidence that the original stabilised peat is being redistributed from a higher level over a lower zone which follows the peat margin. It is this redistributed peat that the Nardetum colonizes, forming a zone marginal to the peat mass. What has happened to the peat to bring about this sharp contrast between moor vegetation and Nardetum is not clear. The surface peat is certainly redistributed, so that one no longer finds the stratification present in undisturbed peat. The commoner case is to find the redistributed peat lying directly on a substratum of stones, sand, and clay. Less often the redistributed peat lies over a substratum of older peat still showing stratification, or with tree remains embedded in its basal layers. Provisionally it is suggested that the Nardetum is favoured by chemical and physical changes arising from the redistribution of the peat. This process would favour oxidation, so that the original raw humus of peat is carried a stage nearer to the final decomposition products characteristic of vegetable mould. Accompanying this there might be some liberation of nitrogen and of the mineral bases which are locked up and non-available in raw humus. But the liberation of such fertilisers cannot be great because *Nardus* is generally regarded as an indicator of poor soils, and our experience is that flushing with water relatively rich in mineral matter displaces *Nardus* and brings a sward of finer grasses (Pl. II, Fig. 2); other effects of manuring *Nardus* are given later. Another result of the redistribution of peat may be a change in the colloidal character which affects the water content¹. A solution of the problem along edaphic lines seems the more probable. The Nardetum is too widely distributed to be traced directly to climatic or topographic factors. Nor can we find sufficient evidence to support the suggestion of several authors that sheep-grazing is directly responsible for invasion by the Nardetum. So far as the Nardetum marginal to peat is concerned, the factors involved in the redistribution of the peat appear to be the effective ones. There are many indications that land now occupied by Nardetum was formerly peat-covered; on the other hand it does not follow that all areas of Nardetum have arisen in this way.

ECOLOGY OF *NARDUS STRICTA*.

The chief characteristics of *Nardus* are here briefly summarised from various sources (Stebler and Schröter (14), C. Schröter (12), C. Raunkiaer (10), etc.). This grass is widely distributed from the mountainous areas of southern Europe and the plains of northern Asia onwards to West Greenland in the Arctic. In Europe it is included by Chodat as "Ubiquist,"

¹ This JOURNAL: Notices of Publications, 2, pp. 174 and 209, 3, pp. 178, 229, etc.

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since it appears to be as much at home in the lowlands as amongst the hills. In Scotland *Nardus* decreases distinctly on the higher hills of the Highlands, although patches may occur at altitudes over 3000 feet (1000 metres).

The vegetative organs form very compact tufts made up of a system of horizontal rhizomes almost on the surface of the soil. The leafy and flowering shoots are firmly enclosed in thick tough basal sheaths which persist long after the foliage is dead, and these form the double or triple series of comb-like-teeth so characteristic of the rhizomes. The frequent branching of the rhizomes and the closeness of the shoots lead to considerable congestion, and as new organs are formed they become piled on the remains of the old ones; thus tussocks are formed which we have seen knee-high. Plant remains and wind-borne detritus are added, hence a colony of *Nardus* generally forms a thick mat or sod which extends peripherally and ousts all but a few rivals such as *Juncus squarrosus*, *Vaccinium myrtillus*, and in wet places *Molinia caerulea*. The humus mat furnishes, however, a substratum for shallow-rooted humus-frequenting species, such as *Deschampsia flexuosa*, *Agrostis* spp., *Anthoxanthum*, *Luzula campestris* (vars.), *Galium saxatile*, *Potentilla erecta*, etc. The roots of *Nardus* are thick and cord-like, and the finer lateral roots are mycorrhiza with an endotrophic fungus. These are also features of the moor and heath grasses *Molinia caerulea* and *Triodia decumbens*, and it seems natural to correlate such roots with a humus substratum. *Nardus* is distinctly xerophytic with its thick basal sheaths, involute leaves, thickened epidermal structures and protected stomata.

Some indication has already been given of the wide range of substrata frequented by *Nardus*. The habitat conditions may be examined further through the influence of agents which have been used in controlling *Nardus*:

(a) *Influence of spring water.* We have frequent records that a "flush," the emergence of a spring on the Nardetum zone, brings a greener vegetation, characterised in the hill districts by *Festuca ovina*, *Agrostis alba*, *Cynosurus cristatus*, *Holcus lanatus*, and other grasses, along with a number of other species including *Trifolium repens*, *Ranunculus repens*, etc. (Pl. II, Fig. 2). Somewhat similar is the alluvial grassland which follows the flood margins of streams from the Nardetum downwards. During summer these streams are maintained by springs, because in a normal summer peat no longer gives off water, and any streamlets from the neighbourhood of peat will be found to be more or less "hard" water. This is a marked feature in areas with a complex and crumpled geological structure, including various types of more soluble rock, such as occur in the Silurian of southern Scotland and throughout most of the Scottish Highlands. The influence of spring water in restricting the Nardetum is also a marked feature of Mountain Limestone districts. The effect of irrigating Nardetum with glacier water is recognised in Switzerland as a means of improving the grazing of the meagre and unpalatable *Nardus* vegetation. Brockmann-Jerosch (2, p. 306) gives comparative lists

of the herbage of a *Nardus* grassland with and without irrigation; the effect is to reduce *Nardus*, *Vaccinium*, etc. and to increase the proportion of better grasses (*Poa* spp., *Phleum alpinum*, *Festuca rubra*) and other herbage (*Trifolium repens*, *T. pratense*, *Ranunculus* spp., etc.). J. Braun (1, p. 137) states that irrigation converts a sward of *Nardus* into *Agrostis vulgaris*. The converse case of irrigating alluvial grassland with water from peat may be observed where the discharge from surface drains from peat flows down a grassy stream bank; the line of flow is indicated by *Nardus*.

(b) *Manuring*. Stebler and Schröter (14) state that manuring with farmyard manure quickly ousts *Nardus*. We have seen no case of direct manuring in this way without previous ploughing, but it is not uncommon to find knolls or slopes within the Nardetum which sheep use as lairs and thus manure heavily; the effect is to replace *Nardus* by a close grassy herbage.

(c) *Grazing*. No stock graze *Nardus* by preference if other types of herbage are available, but in early summer there is a certain amount of grazing on the younger foliage of the Nardetum. The influence is more perceptible after a course of grazing by hardy hill cattle, whereby the *Nardus* becomes less tufted and forms a closer sward with a larger proportion of other plants. If the cattle are restricted by fencing, the herbage becomes less distinctly *Nardus* and more useful economically, but areas grazed in this way are not common¹. Early in the season uprooted tufts of *Nardus* and *Juncus squarrosus* are frequently seen where grazing takes place, but this has little effect on the herbage unless the grazing is continuously maintained. It has been stated by some authors that an increase of *Nardus* results from grazing. It is well known that *Calluna* is destroyed on tracks across the Callunetum, *Nardus* frequently replacing it in drier places, *Molinia* in wetter parts. Graebner (4, pp. 122 and 168) refers to increase of *Nardus* as a result of grazing, and states that the larger areas of Nardetum in North Germany are places long grazed. J. Braun (1) from observations on the Massif de l'Aigoual concludes that the extension of the Nardetum is a result of excessive grazing by sheep. The area long used for pasturage is an extremely poor Nardetum. This is clearly defined from ungrazed areas where *Deschampsia flexuosa* with many flowering plants forms a luxuriant sward, which represents the first stage towards reconstruction of beech forest as the result of protection from grazing. The evolution of the Nardetum is a survival of the fittest, only the plants more resistant to grazing are maintained. These observations indicate that *Nardus* when actually grazed (or mown) tends to be checked, but that indirectly the continuous grazing of a mixed vegetation, including *Nardus*, tends to eliminate certain plants and to favour others, notably *Nardus*, in habitats where the substratum is suitable. As regards the Nardetum marginal to peat, now under consideration, its distribution cannot be traced

¹ Stebler and Schröter state that when a Nardetum is regularly mown, *Nardus* is suppressed, and conversely if left unmown it increases.

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to excessive grazing. The sheep are not confined to the Nardetum, because the grazing area of a flock-unit is arranged to include various types of herbage (flush and alluvial grassland, Callunetum, Eriophoretum, etc.). It has frequently been noted that while other types of herbage are dotted with sheep, the Nardetum is avoided. Nor is there any need for excessive grazing, for the number of sheep assigned to an area of rough hill pasture is rarely one sheep per acre, and is frequently three acres per sheep, and on the higher hills the grazing season for the Nardetum extends at the most from April to November.

(d) *Burning*. The direct effect of burning the Nardetum periodically is to reduce the tussock character of *Nardus*, to increase its grazing value, and to favour a larger proportion of other grasses and herbage. This effect is the more marked the oftener the burning is done, because *Nardus* is only affected for one year and soon resumes dominance. We have seen the herbage of the Nardetum maintained in excellent grazing condition by periodic burning every two or three years. Indirectly, moor burning may be responsible for the extension of *Nardus*. The Callunetum or heather vegetation is the plant association to which most attention is given, and every year considerable areas of this are burned over in spring. The object is to destroy old heather and to encourage the growth of shorter and more vigorous heather for grouse and sheep. When *Calluna* is burned while still vigorous (the period varies from 10 to 15 years) the recovery is rapid, and in two to four years there may be a close carpet. But when the heather burned is aged (generally over 20 years), the recovery is slow, and meanwhile a series of colonising plants take possession; these include *Vaccinium myrtillus*, *Erica tetralix*, *Deschampsia flexuosa*, *Agrostis vulgaris*, *Galium saxatile*, *Pteris aquilina*, *Molinia caerulea*, or *Nardus*, according to the type of soil. *Nardus* tends to colonise soils with a peaty surface; and where *Calluna* does not recover for several years¹, *Nardus* may form extensive patches which tend to remain permanently as centres of invasion. It is a common opinion that hills which once carried heather are now covered with Nardetum. It is also the case that during the years after burning the humus covering is much wasted, and this favours the Nardetum.

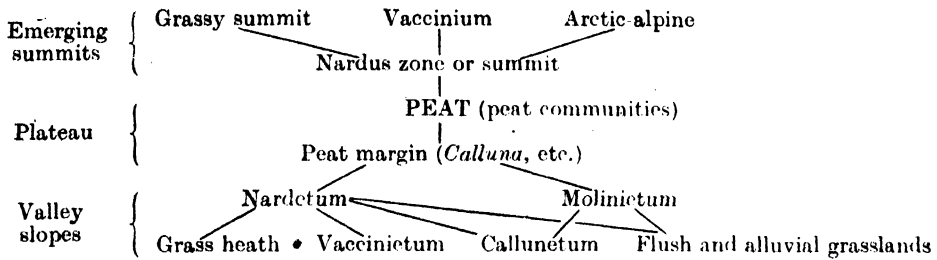
NARDUS PLANT COMMUNITIES.

The charting of plant communities with abundance of *Nardus* presents some difficulty in the field. Transitions to other moor and heath types are gradual and may cover extensive areas. In dealing with such transitions it is necessary to have a standard series of fixed types, that is types which are easily recognisable and have a relatively fixed composition. Some of these fixed or stable types are already recognised in vegetation surveys, e.g. Callunetum, Eriophoretum, Vaccinietum, etc. In the more recent surveys we

¹ Places burned ten years ago have been observed still almost devoid of heather.

have found it necessary to establish other types which break up the hill pasture or rough grassland into associations more indicative of their economic utilisation.

The following is now used as the ground-plan for the northern hills (see Fig. 1).



The peat plateau is a convenient base-line for hill surveys, because it occurs on almost all the lower hill-ranges of central Britain, and the topography is such that the peat plateau occurs at altitudes round about 2000 feet (610 m.), as on the Pennines, the various hill-ranges of the Border country and southern Scotland, the central ranges (Sidlaws, Ochils, Campsie Fells) of Scotland, and the foot-hills of the Grampians. On these and similar ranges, a few isolated summits, generally limited in area, rise above the peat plateau, while below it the valley slopes descend to some stream. In the Highlands peat deposits are still more extensive, but it is only where the watershed area is broad and relatively flat that peat forms a summit plateau, e.g. the 3000 foot plateau on the boundaries of Forfar, Aberdeen, and Perth. More frequently the plateau topography is interrupted by a range of rounded or conical summits, hence the distribution of the peat takes the form of terraces on the slopes, and peat-bogs often with bog-pools (dubh-lochans of Crampton), between the summits.

Passing upwards from the peat, the Nardetum on redistributed peat forms a zone marginal to the peat. Where retrogression of peat is far advanced, as on the lower ridges, the Nardetum may occupy the summit (Plate II, Fig. 2)¹. Complete erosion of the peat leads to disappearance of *Nardus*, and the summit vegetation of the lower ranges is characterised by pure *Vaccinietum*, or by a turf (more or less complete) of grasses, *Vaccinium*, etc., all in a dwarf condition and with a considerable proportion of xerophytic mosses and lichens. In the Highlands the higher summits are occupied by the arctic-alpine plant formations (15). Most of them have probably never been peat-covered, but where erosion of peat can still be seen in progress on the 3000 foot plateau of the Aberdeenshire hills, the place of *Nardus* is taken by a close sward of *Carex rigida* and dwarf grasses (e.g. forms of *Festuca ovina*, *Deschampsia caespitosa* and *D. flexuosa*).

¹ The *Nardus* summit is referred to in several of the British Botanical Surveys, e.g. **W. G. Smith** and **W. M. Rankin**, *Yorkshire*, Part II, 1903; **W. G. Smith**, *Forfar and Fife*, 1904-5; **C. E. Moss** (1913), p. 193.

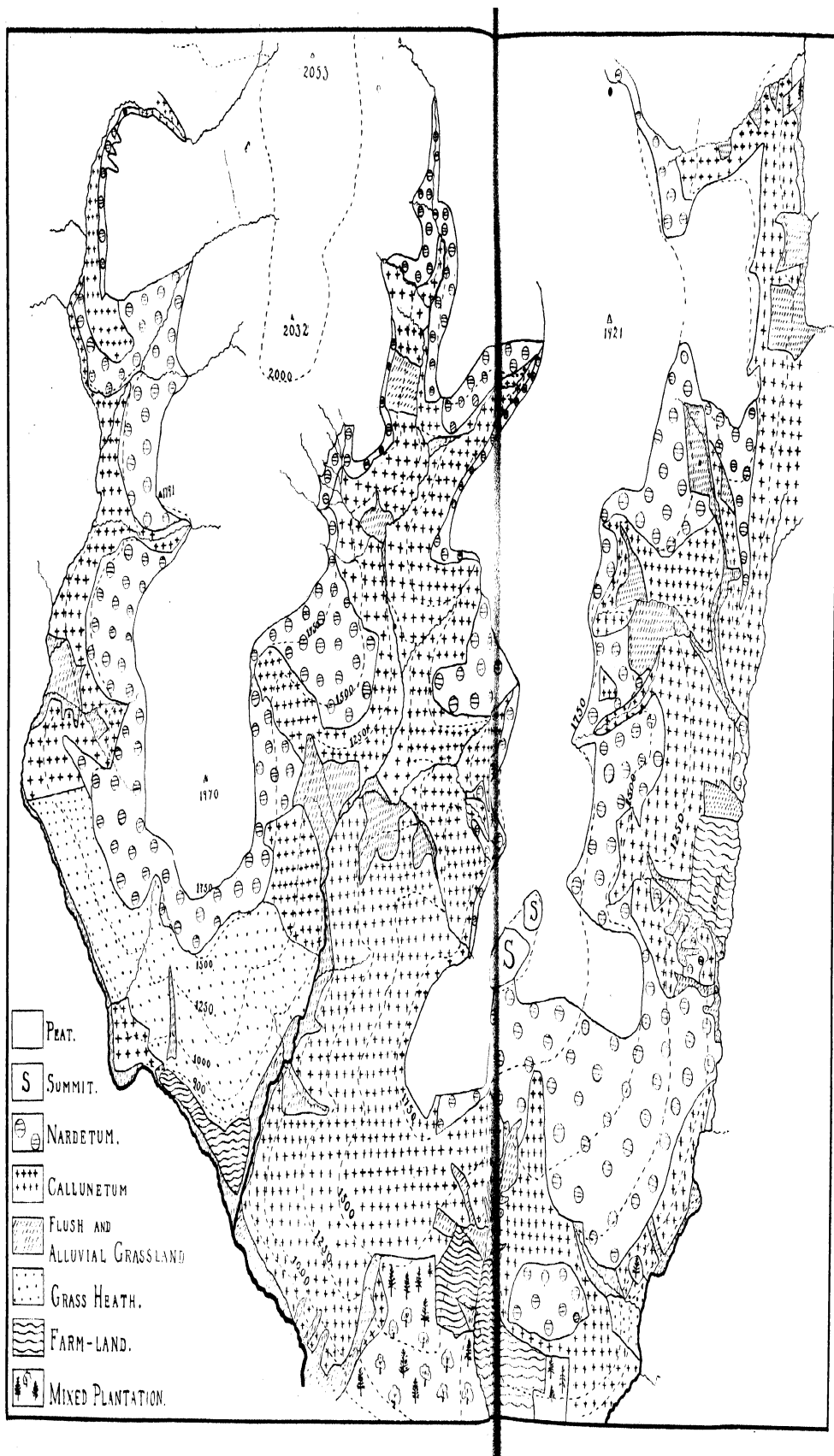


FIG. 1. Vegetation map showing part of the Moorfoot Hills, Peeblesshire, reduced from six-inch field maps. (1:23050 or approx. 3 inches to one mile.)

The main watershed towards the north (top) is peat with isolated summits, of which only one spur-summit (S) lies within the area. The three streams flow southwards from the water-shed, and join to form the Leithen Water, a tributary of the Tweed; in the upper right-hand corner a stream flows northwards. The vegetation of the middle valley is shown on both banks, that of the east and west streams on one bank only. Contour lines in feet (= 328 metres) are dotted, except where the contour has been taken as the boundary of a plant association. The vegetation of the peat is described on pp. 2-4; that of types other than Nardetum on pp. 9-12.

10 *The Distribution of Nardus stricta in Relation to Peat*

Below the peat zone the Nardetum abuts on the six fixed types shown in the scheme, and presents transitions to each. The area selected (Fig. 1) shows the Nardetum adjacent to four types, the other two are present but not extensively enough to be mapped. In order to ascertain the composition of the Nardetum, a plant census was made from forty-eight lists in which *Nardus stricta* is a dominant or a conspicuous species. Nineteen of these lists from our *Nardus* zone show a marked dominance of *Nardus* alone, and the following is regarded as the composition of the typical Nardetum marginal to the peat zone:

Nardus stricta, L. Dominant. (19)¹

<i>Deschampsia flexuosa</i> , a. (18)	<i>Vaccinium Myrtillus</i> , o. to l. d. (17)
<i>Agrostis</i> spp. ² a. (17)	<i>Calluna vulgaris</i> , o. to l. a. (10)
<i>Anthoxanthum odoratum</i> , o. to a. (11)	<i>Juncus squarrosus</i> , o. to l. d. (12)
<i>Festuca ovina</i> , or <i>F. rubra</i> ³ , o. to a. (9)	<i>Luzula multiflora</i> , o. to a. (12)
<i>Galium saxatile</i> , o. to a. (14)	<i>Molinia coerulea</i> , o. to a. (4)
<i>Potentilla erecta</i> , o. to a. (14)	<i>Polytrichum commune</i> , a. (6).
Less abundant species:	
<i>Carex Goodenowii</i>	<i>Sphagnum</i> spp.
<i>Carex binervis</i>	<i>Aulacomnion palustre</i>
<i>Eriophorum vaginatum</i>	<i>Dicranum</i> spp.
<i>Blechnum spicant</i>	<i>Campylopus</i> spp.

The remaining lists in the plant census show *Nardus* as a co-dominant, a subdominant, or an abundant species. The species recorded are almost the same as in the Nardetum, with this difference that there is an increase in the dominance of the characteristic species of some other type, e.g. *Molinia*, *Calluna*, *Vaccinium*, etc. It is a feature of the Nardetum lists that the species are all widely distributed, not only according to distribution in area, but also as regards distribution through various plant communities. The lists might be described as lacking in character, since there are no "endemic" species.

As a working hypothesis, we assume that a co-dominance of *Nardus* with *Calluna*, *Molinia*, etc. indicates a transition zone. Such a zone may indicate one of two things. It may mean that a temporarily dominant plant (cf. *Psamma* in the sand dune formation) is in process of displacement by some plant community later in the succession. Transition may also mean that the

¹ Figures in brackets show the number of times the species was recorded. The number of lists could be considerably increased, but after the composition of the Nardetum had been ascertained the records became limited to "*Nardus* as usual."

² *Agrostis vulgaris* is the more frequent species, but there is much variation in the specimens examined. Some forms might be referred to *Ag. canina*, others agree more closely with the type generally described as *Ag. alba*.

³ *Festuca ovina* and *F. rubra*. Considerable variation has been observed in these species. The more abundant type is that with "diageotropic innovation shoots," so that, according to Hackel, this is *F. rubra* L. sens. ampl. It is not uncommon to find tufts with "apogeotropic" shoots arising intravaginally in the sheaths of the lower leaves; this comes within Hackel's *F. ovina* L. sens. ampl. The leaf-form is always bristle-like, but there is great variation from "setaceous" to "juncate." Recent investigations (Lindhard, E., *Tidskrift f. Landbrugets Planteavl*, Bd. 20, pp. 1—23, 1913) show that perennial grasses mature more seed when cross-pollinated, and that within most species are included many forms which remain true on cultivation. It is therefore probable that there is considerable variation of forms in most of the natural associations which include grasses.

substratum presents local edaphic variations, so that one part is, say, moister while another is drier, as in the case of retrogressive peat already described. Both kinds of transition may exist in the case of *Nardus*. *Nardus* is the first phanerogamic invader of redistributed peat, and it may be displaced by another plant community. The experimental observations already given support this view. The Nardetum also represents a phase in the retrogression of peat, but as the process does not go on equally over the whole area there may be considerable local variation within a small space. It is the case that on hill pastures with *Nardus* there is often an almost bewildering change in the plant grouping from place to place. This would seem to indicate that the edaphic conditions necessary for the various species are not very distinctly differentiated, and that the chief constituents of the vegetation are species with a wide range of adaptability.

TRANSITIONAL ASSOCIATIONS.

The types of vegetation which abut on and form transitions with the Nardetum are, briefly, as follows:

A. Molinietum. The factors determining the distribution of *Molinia caerulea* have been examined by T. A. Jefferies (6), mainly in West Yorkshire. The Molinietum is also well represented in the Moorfoots and other areas. Our observations confirm the conclusion of Jefferies (p. 99) that "the distribution of *Molinia* depends primarily upon an abundant supply of relatively fresh water—whenever stagnation becomes pronounced, so that the water is badly aerated and excessively acid, *Molinia* tends to degenerate." The same author demonstrates that *Molinia* grassland is intermediate between Nardetum and Eriophoretum so far as water supply and acidity are concerned. We would emphasise his distinction as regards the water. Where the water is mainly from peat or surface drainage, the succession is from peat vegetation (Eriophoretum and Scirpetum caespitosi) through the more ericaceous vegetation of the peat margin, to Nardetum. This is also the succession where springs from below the peat pass into deepened water channels, or emerge on the slopes below the Nardetum zone. Where, however, the springs emerge so that they irrigate the marginal peat, then the Molinietum comes into evidence. Our observations on the substratum of the Molinietum show a strikingly constant occurrence of about nine inches of peat¹, which remains distinctly moist throughout the summer when the Nardetum peat is drier. Another feature is that the Molinietum is developed more frequently along unbagged margins of peat, whereas Nardetum is characteristic of a margin of peat hags. The distribution of *Molinia* thus depends mainly on the occurrence of spring water, and hence it is not uncommon to find tracts of Molinietum not directly related to the peat margin, but isolated among other associations. In the majority of cases the Molinietum probably represents the residue of a former peat-covered

¹ The depth of peat or humus was tested constantly by the staff throughout this survey, and is recorded for most of the plant associations.

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area, the peat being preserved from erosion by its more constant but not excessive moisture. In other cases there is reason to believe that the existing peat is largely an accumulation from the Molinietum itself. The Molinietum in its typical form shows a complete dominance of *Molinia*, but this may pass gradually through a transition zone into pure Nardetum marginal to peat. Our interpretation of the transition zone is that it is Nardetum irrigated by spring flushes, or conversely a Molinietum imperfectly flushed so that *Nardus* and other species of drier substrata find a place¹.

B. Flush and alluvial grassland. This is generally well defined from the Nardetum. The uppermost alluvial grassland occurs between the Nardetum and the stream along the flood-margins of the headwater stream-lets²; here it may be more or less mixed with *Nardus*. This grassland forms a marginal zone distinguished by dominance of grasses, with frequent occurrence of sedges (*Carex*), rushes (*Juncus*) and other moisture-loving species. The flush grassland vegetation occurs where springs emerge in the Nardetum (Pl. II, Fig. 2) and other types; if the springs are intermittent throughout the summer, *Nardus* may be an abundant species.

C. Callunetum. This extensive association is typical of the drier and steeper valley slopes (Pl. II, Fig. 1). As a rule there is a zone of Nardetum between this zone and the vegetation of the peat margin where *Calluna* "on peat" may again be abundant. Sometimes, however, *Calluna* is so abundant from the peat margin downwards that the Nardetum falls out³. During the survey three types of Callunetum were distinguished as regards depth of peat, time of recovery after burning, and economic value, but this is not the place for details. *Nardus* enters into competition with *Calluna* in all three, and *Molinia* in the case of two.

D. Vaccinietum. This occurs as a dwarf summit vegetation, and as a taller growing type on steep dry valley slopes. It is an extensive association in the Highlands, and was mapped by R. Smith as Vaccinietum. *Nardus* may occur abundantly in those parts of the zone which lie towards the peat margin.

E. Grass Heath. This vegetation has been met with extensively on steep dry valley slopes in south-eastern Scotland (Map). It consists largely of *Deschampsia flexuosa*, *Agrostis* spp., *Galium saxatile*, *Potentilla erecta*, *Vaccinium myrtillus* (dwarf), but the chief feature is a dense undergrowth of mosses of drier habitats. These last were so abundant in analyses of representative turfs, that mosses formed the larger part of the air-dried herbage. In the upper part of this zone towards the peat margin, *Nardus* may become abundant or subdominant; this transition was very marked in case of the grass heath shown in the map, Fig. 1.

¹ The influence of spring flushes on moorland vegetation is a topic for a future paper in which the Molinietum will appear as a type of flush.

² This zone is too narrow to show in field maps.

³ Several places showing this will be found on Fig. 1, by following the peat margin; most of these have much *Nardus* mixed with *Calluna*.



Fig. 1

D. M. phot.

NARDETUM MARGINAL TO AND INVADING THE PEAT PLATEAU OF THE MOORFOOTS (see pp. 2 to 4). The darker vegetation is on peat, the lighter is Nardetum which is continued down the slope to a streamlet. A portion of Molinietum is seen in the bottom right-hand corner. The distant summit is about 2000 ft. (600 m.) altitude.



Fig. 2

D. M. phot.

NARDETUM WITH VESTIGES OF THE PEAT MARGIN SHOWING PEAT HAGGS (see pp. 2 and 3). Northern Moorfoots, about 600 m. alt., September, 1914.

SUMMARY.

Nardus stricta is a frequent species, with varying degrees of dominance, in the hilly parts of northern Britain. Among other plant associations, where it is conspicuous, it is the dominant species in an association (Nardetum) which forms a zone marginal to areas of retrogressive peat. Nardetum occurs typically on peat which has been redistributed from the exposed surface of peat hags by water, wind, and biologic agents, so that it is no longer part of the original peat mass, but forms a zone marginal to the mass. This zone is rapidly invaded by *Nardus* which from its mode of growth and structure is adapted to withstand the conditions of this habitat. This Nardetum is a relatively fixed or stable type of vegetation so long as the edaphic conditions remain constant, and it is extensive enough in the subalpine region of the central and northern hills of Britain to warrant its being recorded on vegetation maps of "six-inch" scale. From the economic aspect it is a zone of relatively low grazing value.

The recognition of this Nardetum is part of a segregation of what in the earlier vegetation surveys in Britain was described as "hill pasture" or by other titles indicating the greener vegetation as distinguished from Callunetum, Eriophoretum, Vaccinietum and other types. The segregation is carried still further by other types briefly described: (1) Flush and alluvial grasslands; (2) Grass heath; (3) Molinietum. These units of "hill pasture" are based on the composition of the vegetation, but they also represent an economic value with reference to grazing. These types of grassland occur in consecutive and extensive areas so that they can be charted as units of the uncultivated land of the subalpine region.

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THE OAK-HORNBEAM WOODS OF HERTFORDSHIRE PARTS III AND IV¹

By E. J. SALISBURY

(With two Figures in the Text and XX Tables)

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PART III. THE *QUERCUS SESSILIFLORA*-*CARPINUS* WOODS

(1) General and Introductory

The *Quercus sessiliflora*-*Carpinus* woods, with which the present part deals, comprise some of the largest woodland areas in Hertfordshire and together occupy between two and three thousand acres. For the purposes of this account a few woods have been included in which *Quercus robur* is present in preponderating numbers, but where there is good reason for believing this condition to be the outcome of planting. But, in estimating

¹ Parts I and II appeared in this JOURNAL, 4, pp. 83-117.

the distinctive characteristics of this type, and the frequencies of the constituent species, reliance has been chiefly placed upon observations in the woods at Symond's Hyde (ca. 220 acres) and Sherrard's Park (ca. 250 acres), in which the Oaks are almost exclusively *Quercus sessiliflora*. These two woods have been visited many times at frequent intervals over a period of from three to four years. The necessity for such repeated visits, at all events throughout the vegetative season, cannot be too strongly urged if reliable data as to frequencies are to be obtained. This is all the more important since many of the herbaceous species are common to several types of woodland, but exhibit a prevalence peculiar to each. In addition to the two woods named a further area of considerably over 1000 acres has been carefully examined though at longer intervals.

It is with great pleasure that the author records his indebtedness to the Rt. Hon. the Marquis of Salisbury, Lord Lytton, Sir George Faudel Phillips, the Hon. A. Holland-Hibbert, Lt-Colonel A. D. Ackland, Major Smith-Bosanquet, and other owners for permission to investigate their woods. His thanks are also due to Mr Septimus Beck and to Mr J. C. McCowan for their kindness in affording information with regard to the estates of which they have charge.

For assistance in the determination of Algae, Fungi, and Lichens respectively the author is indebted to the following specialists: Prof. F. E. Fritsch, D.Sc., Mr J. Ramsbottom, M.A., and Mr R. Paulson, F.L.S. The surveys reproduced in Figs. 1 and 2 were kindly prepared by the author's brother Mr A. H. Salisbury, M.S.A.

(2) The Edaphic Conditions

Attention has previously been called to the general distribution in Hertfordshire of the various types of Oak-woods (Salisbury, *loc. cit.*, p. 84). As already stated, the *Quercus sessiliflora*-*Carpinus* woods predominate in the south-west of the county, but they are in addition generally associated with superficial deposits, geologically different from those in which *Quercus robur* is the dominant tree (cf. Table I). The latter woods occur chiefly on the clay-with-flints, whilst the woods here dealt with are found mainly on outliers of the Reading beds, the London Clay, Glacial Gravel, or Boulder Clay. Information regarding the geology of the district has been kindly furnished by the author's friend Mr G. W. Lamplugh, F.R.S., and Dr Sherlock of H.M. Geological Survey, the latter of whom has recently mapped a large part of the area in question.

An interesting case is afforded by the Devil's Dyke, near Marford, reputed to be a pre-Roman earthwork (cf. *Historical Monuments of Hertfordshire*) which occupies an isolated patch of what Dr Sherlock regards as probably Boulder Clay. The dyke is about a quarter of a mile long and some 35 ft deep, with steep wooded sides. At the present day *Quercus sessiliflora* is

entirely absent, but a careful search has revealed two specimens of the hybrid Oak. There are no woods in the immediate vicinity and those which lie nearest contain no *Quercus sessiliflora*. Evidently then *Q. sessiliflora* must formerly have been present, but probably this, like so many of our woods, has been replanted with *Q. robur*, only a few of the original sapling hybrids having survived. The general character of the flora in other respects (e.g. frequent Beech and abundant Holly) suggests a *Q. sessiliflora*, rather than a *Q. robur* wood. This exemplifies the replacement that has probably taken place in several instances (e.g. Balls Wood, Hertford).

It is perhaps nothing more than a coincidence that *Q. sessiliflora* is by far the commoner Oak in Grimm's Dyke, another pre-Roman earthwork, near Wigginton.

It should be noted that both in Hawkshead Wood (North Mimms), and in Oxhey Woods, the local dominance of *Q. sessiliflora* is associated with Reading bed outliers (W. Whitaker, *Mem. Geol. Survey*, vol. 1, pp. 198-203, 1889), and here too human interference may have considerably reduced both the number of individuals and the area occupied by this species. On the other hand *Q. sessiliflora* does occur in small numbers where there is no reason to suppose the present relative frequencies to have been artificially produced. For example, Pryor's Wood, near Ayot, situated on the Clay-with-flints, contains a few Durmast Oaks, but the general character of the flora is entirely that of the *Q. robur-Carpinus* type.

A striking instance of the effect of geological conditions is seen at Symond's Hyde. Here we have a group of contiguous woods, namely Cox's Wood, Titnol's Wood, Great Wood, and Furze-field Wood, which in the order named extend from the higher to the lower ground. The valley is occupied by a loamy boulder clay which gradually thins out as we pass up hill and finally gives place to Clay-with-flints just beyond Cox's Wood. In correspondence with this *Q. robur* and *Q. sessiliflora* occur in nearly equal proportions in Cox's Wood; but the latter becomes more abundant as we pass down hill, so that in Symond's Hyde Great Wood the common Oak is quite rare. In Hitch Wood and Wain Wood, in the north of the county, *Q. sessiliflora* is fairly common, although both according to the old drift maps are situated on the Clay-with-flints.

In connection with the presence of this type upon the Boulder Clay, it should be noted that the latter is often not typical and as it occurs in these woods is frequently a relatively light soil of a loamy character. Possibly washing out of the finer particles from the upper layers has contributed towards this (cf. Whitaker, *loc. cit.*, p. 321), a factor that has also operated in the London Clay areas. In reference to the latter Mr Whitaker mentions that "the upper beds like the basement bed are more sandy than the large mass of the formation" (*loc. cit.* p. 239). Sherrard's and Brock's Woods furnish examples of woods situated mainly upon the Woolwich and Reading

Beds and the same is true of the Ruislip Woods in Middlesex. In all these, the dominant tree is *Quercus sessiliflora* and the undergrowth is chiefly Hornbeam. Still more significant is the occurrence of a similar relation elsewhere. Thus we find the scattered woods near Reigate in Surrey illustrating the same feature. Margery Wood situated on the Clay-with-flints is a typical example of the *Quercus robur-Corylus* type whilst the isolated patches of Reading and Woolwich Beds near Headley are occupied by *Quercus sessiliflora-Corylus* woods with a ground flora that is strikingly similar to that of the *Q. sessiliflora-Carpinus* woods of Hertfordshire.

The enumeration (Table I) shows that this type is then characteristic of Boulder Clay, Glacial Sands and Gravels, and the sandy soil of the Woolwich and Reading Beds. Moreover the composition of the herbaceous flora in areas of scrub bears out the natural relations of the vegetation to these different soil types (cf. Salisbury, "Ecology of Scrub," *Trans. Herts. Nat. Hist. Soc.*, vol. xvii, 1918).

TABLE I. *Geological Character of Soils*

Wood	Type	Geological character of soil
Sherrard's Park	<i>Q. sess.-Carp.</i>	Boulder Clay and Reading Beds
Brook's	" "	" " "
Symond's Hyde Great Wood	" "	Boulder Clay
Titno's	<i>Q. sess. + Q. robur-Carp.</i>	" "
Blackboy	" " "	" "
Mardley Heath	" " "	Glacial Gravel
Ninning's	" " "	Glacial Gravel and Sand
Harmer Green	" " "	Boulder Clay. Woolwich and Reading Beds
Burnham Green	" " "	Reading Beds, Gravel and Sand
Bramfield	" " "	Boulder Clay
Punchett's	" " "	Glacial Gravel and Boulder Clay
Knebworth (Gt. Wood)	" " "	Glacial Gravel and Clay-with-flints
Wain	(<i>Q. robur d. + Q. sess.-Carp.</i>)	Clay-with-flints
Hitch	" " "	" " "
Broxbourne	(<i>Q. sess. + Q. robur</i>)	London Clay with patches of sand and Gravel
Cow Heath	(<i>Q. sess. + Q. robur</i>)	London Clay
Wormley	<i>Q. sess.-Carp.</i>	" "
Ruislip (Middlesex)	" "	Woolwich and Reading Beds.

A pronounced feature of these woods is the fact that in spite of the coarse texture of the soil they are, compared with the woods of common Oak, extremely wet in winter, a feature well shown by the presence of free water upon the paths and by the character of the path-flora. The not infrequent presence of Beech indicates that the upper layers of soil are relatively dry, since this tree is very intolerant of inundation. One can only conclude therefore that the permanent water-table approaches very close to the surface, so that the slight depression due to the paths, together with the greatly increased water-capacity and capillarity of their soil, resulting from compression and accumulation of finer particles, produces the water-logged condition.

The same general relations as regards types of soil have been found to obtain elsewhere. Thus Wilson ("Plant-distribution in the Woods of North-east Kent," *Ann. of Bot.*, vol. xxv, pp. 857-902, 1911), in the woods of Kent,

found that, whilst *Q. robur* was the dominant tree on the Clay-with-flints, *Q. sessiliflora* was dominant on the London Clay. The latter species was also the more prevalent on the Oldhaven Beds and Thanet Sands. The *Q. sessiliflora-Carpinus* type has been recorded by Tansley as occurring on the more sandy soils near Hampstead (in *Hampstead Heath, its Geology and Natural History*, chap. II, Vegetation, pp. 85-111, London, 1913), derived from the Bagshot Sands and London Clay.

In general it is only on the lighter types of soil that anything approaching purity of *Quercus sessiliflora* is attained, whilst it is on the heavy London Clay that *Quercus robur* is most frequent in woods of this type. However, the dominance of the latter in some of the woods near Broxbourne is probably an outcome of planting.

Usually the soil of these woods is a loam, and mechanical analyses show (cf. Table II) that even in the damper societies the proportion of finer particles

TABLE II. *Mechanical Analyses of Woodland Soils*

Wood	Type	Ground Society	Fine Gravel %	Coarse sand %	Fine sand %	Silt and clay %
Stocking's ...	Q. robur-Carp. ...	Ficaria -	2.4	15.8	21	45.2
Oxhey Grange ...	" " ...	Mercurialis	0.8	26.48	19.2	50.64
Stocking's ...	" " ...	Anemone	4.2	8.6	16.2	63.36
Oxhey ...	Q. robur + Q. sess.-Carp.	Pteris ...	8.8	21.0	25.4	35.6
Broxbourne ...	Q. sess.-Carp. ...	Path ...	4.8	19.0	23.4	42.0
Brock's ...	" " ...	Mercurialis	1.48	11.2	42.52	38.24
Sherrard's ...	" " ...	Nepeta ...	6.2	32.68	22.4	31.0
Brock's ...	" " ...	Rubus ...	5.32	46.72	17.76	21.96
Sherrard's ...	" " ...	Scilla ...	6.8	52.4	15.88	18.72
Wormley ...	" " ...	Pteris ...	8.2	21.0	31.2	20.0
Brock's ...	" " ...	Pteris ...	2.2	51.48	21.12	17.76
Average for <i>Q. robur</i> woods ...			2.46	18.29	18.8	53.06
Average for <i>Q. sessiliflora</i> woods ...			5.0	33.49	24.89	27.09

is usually only comparable to that in the drier societies of the *Q. robur* woods. The amount of clay and silt ranges from about 18 % in the lighter soils to 42 % in the wetter parts, namely the paths. That the determining factor for the dominant tree is not here depth of soil (cf. Moss, *Vegetation of Peak District*, pp. 45, 46) is clearly indicated by an examination of the pits which are often present. In these it can be seen that the soil overlying the chalk is at least 16 ft in depth, and at Bricket Wood the Boulder Clay reaches a thickness of about 40 ft (T. E. Lones, "The Gravels, Sands, Clays, and Loams of W. Herts.," *Trans. Herts. Nat. Hist. Soc.*, vol. x, p. 163, 1900). Moreover where the soil thins out, as on some of the lower valley slopes, there is a tendency for *Q. robur* to become more frequent rather than less so, perhaps owing to the increase of moisture and the lower acidity of the soil.

Humus. The amount of humus present is comparatively low (cf. Table III). Where the shrub-layer is dense it ranges from 4.8 % to 9.5 % and though sometimes locally higher this is attributable to cumulative peat-formation by certain members of the ground-flora. The latter feature is especially encountered where the bracken predominates, and here the raw humus of the

surface may attain a depth of over 6 in. The total range is 4.8 %–19.4 %, with an average, for all types of ground-vegetation, of 8.5 %, but in general the amount of humus is considerably lower than in the *Q. robur*-*Carpinus* woods.

TABLE III. *Average Organic Content of Soil in different Societies*

Wood	Society	Organic matter %	Range %	Average %
Sherrard's	Pteris	7.5–15.76	5.00–15.76	Pteris 9.92
Brock's	"	7.46		
Symond's Hyde	"	11.06		
Broxbourne	"	7.32		
Wormley	"	10.24		
Cow Heath	"	7.8		
Pinner	"	5.0	5.46–12.2	Rubus 8.25
Sherrard's	Rubus	5.46		
Brock's	"	8.24		
Symond's Hyde	"	6.52–6.54		
Wormley	"	12.20		
Broxbourne	"	10.56		
Sherrard's	Nepeta	6.9–7.50	6.32–19.4	Nepeta 7.08
Sherrard's	Scilla	6.0–7.28		
Sherrard's	Mercurialis	6.8–11.02		Mercurialis 9.72
Brock's	"	6.56–6.61		
Symond's Hyde	"	11.96–19.4		
Titnol's	"	6.32		
Sherrard's	Ficaria	6.3–11.1	7.44–10.7	Ficaria 8.2
Sherrard's	Path	7.44–8.94		
Symond's Hyde	"	10.1		Path 9.3
Broxbourne	"	10.74		
Wormley	"	9.28		
Sherrard's	Sparse vegetation (dense shrub-layer)	5.36–6.86		
Brock's	" " "	6.16	4.8–9.5	Sparse veg. 6.8
Broxbourne	" " "	8.14		
Wormley	" " "	5.76–8.2		
Symond's Hyde	" " "	4.8–7.0		
Pinner (Middlesex)	" " "	9.5		
Total range			4.8–19.4	
Average of all estimations			8.5	

Water-content. The natural water-content shows an average of about 29.5 % on the dry weight. In summer this may fall as low as 19.3 % or in winter rise to over 53 %, but the differences associated with the different ground-societies remain pronounced despite the seasonal changes in any given locality (cf. Table IV).

TABLE IV. *Natural Water-Contents of Composite Soil Samples from the different Societies*

(a) Sherrard's Wood

Ground Society	Range observed %	Average of all estimations %	Acidities %
<i>Pteris aquilina</i> d.	26.5–45.0	29.9	0.51
<i>Rubus fruticosus</i> d.	19.3–27.0	23.0	0.49
<i>Nepeta glechoma</i> d.	18.5–29.5	26.5	0.45
<i>Scilla nutans</i> d.	23.6–30.2	26.1	—
<i>Mercurialis perennis</i> d.	21.4–34.2	28.7	0.31
<i>Ficaria verna</i> d.	27.6–33.6	31.0	0.12
Path Society	28.8–36.4	33.6	—
Dense shrub-layer and sparse ground-flora	25.3–29.6	26.9	—

TABLE IV (continued)

(b) Various Woods

				%
Symond's Hyde	...	6. xi. 15	Dense Shrub-layer	23.8
"	...	5. iv. 16	"	29.3
"	...	2. iii. 17	<i>Pteris-Rubus</i>	27.0
"	...		(<i>Pteris</i> d.	29.0
"	...	12. x. 16	<i>Rubus fruticosus</i> d.	23.4
"	...		Path (<i>Callitriche</i> , etc.)	37.4
"	...		Dense Shrub-layer	25.5
"	...		(<i>Rubus fruticosus</i> d.	29.8
"	...	1. i. 17	<i>Mercurialis perennis</i> d.	53.4
Titnol's	...		"	27.4
"	...	2. iii. 17	"	32.3
Brock's	...		(<i>Pteris</i> d.	21.9
"	...		<i>Rubus fruticosus</i> d.	27.0
"	...	19. x. 16	<i>Mercurialis perennis</i> sparse	25.4
"	...		" dense	23.2
Wormley	...	17. iv. 16	Dense Shrub-layer	30.2
"	...		"	20.5
"	...		(<i>Pteris</i> d.	29.0
"	...		<i>Rubus fruticosus</i> d.	35.2
"	...	26. x. 16	Path Society	32.6
Broxbourne	...		(<i>Pteris</i> d.	30.1
"	...		Path Society	42.9
"	...		Dense Shrub-layer	30.0
"	...	17. iv. 16	<i>Rubus fruticosus</i> d.	38.0
Blackboy	...	6. i. 16	Dense Shrub-layer	32.7
Cox's	...	13. xi. 15	"	33.2
Sherrard's	...	9. vii. 17	<i>Adora-Ficaria</i>	26.5
Cow Heath	...	10. v. 17	<i>Pteris aquilina</i> d.	25.8
Pinner (Middlesex)	...	28. v. 17	"	24.0
"	"	"	Dense Shrub-layer	35.2
"	"	"	(<i>Pteris</i> Society	28.5
"	"	"	<i>Rubus</i> Society	28.5
"	"	"	<i>Mercurialis</i> Society	31.0
"	"	"	Path Society	35.6
"	"	"	Dense Shrub-layer	27.8
Average for all estimations	...			

Total range in *Q. sessiliflora*-*Carpinus* woods ... 18.5-53.4

Acidity. For only five of the woods have acidity-determinations of composite soil-samples been made, and for these the author is again indebted to Dr H. B. Hutchinson. The range (Tables IV, XII) is from 0.12-0.564 % in the uncut wood, with an average of 0.41 %, as compared with 0.44 % in the *Q. robur*-*Carpinus* woods. The ratio of acidity to humus however shows an average of 1 : 19, as compared with 1 : 29.4 (cf. Part I, p. 91) in woods of the latter type. Evidently then the soil-solution in the upper layers is much more acid than in those woods where *Q. robur* predominates.

Before discussing the significance of these facts regarding the soil it may be well to consider briefly what is known as to the occurrence of *Q. sessiliflora* woods elsewhere. In the Peak district Moss (*loc. cit.*, pp. 45, 46) found that the woods of this species were confined to shallow soils overlying the non-calcareous rocks (sandstones and shales), but both species were found growing together on the deep fluvio-glacial sands and gravels. Moss therefore concluded that depth of soil was the chief factor that determined the dominant

species. *Q. sessiliflora* is the characteristic tree of the steep valley-sides on the Cambrian shales of Wales (Salisbury, *Proc. Linn. Soc.*, p. 3, 1916), on the Old Red Sandstone in the combes of Exmoor, and in the Yorkshire valleys on the oolitic sandstones (Smith and Rankin, "Geog. Distribution of Vegetation in Yorkshire," *Geog. Journal*, p. 13, 1903); in North and Central Wales on Ordovician shales and schists; in Herefordshire on May Hill Sandstone; in Devonshire on non-calcareous Upper Greensand, in the same county and in Cornwall on various Palaeozoic rocks; in Co. Wicklow on Ordovician, in Co. Kerry on Old Red Sandstone, and in Co. Galway on metamorphic rocks (*Types of British Vegetation*, p. 137). This species was also perhaps formerly dominant on the Coal Measure shales and sandstones of Gloucestershire (Tansley and Adamson, "Reconnaissance in the Cotswolds and Forest of Dean," *Journ. of Ecol.*, **1**, p. 86, 1913). In all these cases then the woods occupy soil overlying siliceous rocks, and owing to the steep character of the valley-sides this soil is often very shallow. Moreover, since such situations receive the drainage from the surrounding uplands, the water-content is often high. However, as the writer has pointed out, *Q. sessiliflora* woods do occur locally on calcareous soils, as on the Mountain Limestone of Wales (Salisbury, *Proc. Linn. Soc.*, p. 3, 1916), and the same feature is observed near Symond's Yat (cf. Miss E. Armitage, *Journ. of Ecol.*, **2**, p. 103, 1914).

Probably the presence of *Q. sessiliflora* on calcareous rocks is only rendered possible where the soil has a high water-content either owing to high rainfall or drainage water. It should be noted too that the examples quoted are from Mountain Limestone, the soil-water from which is much less hard than that from chalk.

In view of what has been said with regard to the proximity of the water-table in these Hertfordshire woods it is possible that the soil is rendered physiologically shallow owing to water-logging at a comparatively slight depth. It is however probable that there is some underlying feature common to all these habitats, namely dilution of mineral salts especially carbonates, and accompanying acidity. Where as is most commonly the case woods of this type occupy steep valley sides, leaching out of the mineral salts from the surface-layers is bound to result, an effect all the more pronounced if the soil be shallow. Moreover siliceous rocks are notoriously deficient in soluble mineral substances. It is quite in harmony with this view that *Q. sessiliflora* is chiefly found on calcareous rocks in areas of high rainfall.

The presence of both species in association on the deep fluvio-glacial sands and gravels is perhaps an example of a complementary arboreal society. For the shallow-rooted *Q. sessiliflora* will occupy the upper layers of the soil, deficient in mineral salts, whilst the deeper-rooted common Oak will derive its mineral salts from the lower unleached layers that will have been to some extent enriched by the percolation-water from above. It may well be therefore that the distribution as regards depth of soil is but an expression of differ-

ent demands upon the soil-solution. The lower mineral content of the timber of *Q. sessiliflora* as compared with that of *Q. robur* also argues a capacity for growth in poorer soil.

Hall and Russell (*Agriculture and Soils of Kent, Surrey and Sussex*, pp. 180-183, Board of Agric. and Fish., 1911) give analyses from two woodland soils and a permanent pasture on the Clay-with-flints, and from an old pasture and a common on the London Clay. A comparison of these data from uncultivated land shows that a striking feature of contrast is the absence of lime from the London Clay, though it is only present in small amount in the Clay-with-flints. Also the London Clay is characterised by a low proportion of "available" potash. The normal absence of *Q. sessiliflora* from calcareous soils is therefore in harmony with its presence on the London Clay, both in Hertfordshire and Kent, but the deficiency in available potash may well militate also against the occurrence of *Q. robur*.

A comparison of the amounts of mineral salts present in a number of woodland soils was made by shaking up 50 gms. of air-dried soil in 100 c.c. of distilled water and determining the electrical conductivities of the filtered solutions by means of a Kohlrausch Bridge with Telephone. The results show that generally there is a lower resistance and therefore a larger proportion of mineral salts in the soil-solutions from the *Q. robur* woods (cf. Table XV). If the soil previously heated to 100° C. be employed the adsorption effect of the colloidal particles is largely eliminated and a greater difference between the two types is observed. We are however completely in ignorance as to whether the plant is to any extent capable of overcoming this adsorption effect.

In lowland districts we usually find *Q. sessiliflora* on the drier types of soils, and *Q. robur* on the damper, whilst in upland regions it is woods of the former species which occupy the wetter areas. One of the woods in Hertfordshire, namely Wormley Wood, in which *Q. sessiliflora* is dominant, is reputed to be one of the wettest woods in England, on the other hand parts of Sherrard's wood are dry even in winter. Now we have noted that, having regard to the generally low water-capacity of the soils, the acidity where *Q. sessiliflora* is dominant is greater than in the *Q. robur* woods. The low proportion of carbonates in the soil-solution is probably a great contributing factor to this feature, and it may well be that the effect of the impoverished mineral content is as much indirect through its influence on acidity as direct in its effect on nutrition.

Broadly then, both here and elsewhere, *Q. sessiliflora* may be regarded as a tree tolerant of acid conditions and with a capacity for thriving upon soils deficient in mineral salts. Its rare occurrence on calcareous soils however argues that the present distribution may be rather the outcome of competitive pressure than an expression of natural preference. The frequent paucity of saplings of *Q. sessiliflora* suggests that on soils suitable to either species

Q. robur increases at the expense of its congener (cf. also Salisbury, "The Ecology of Scrub," *Trans. Herts. Nat. Hist. Soc.*, vol. xvii, 1918).

(3) Light-conditions

The shrub-layer in these woods is of very variable density, but in general is either moderately well-developed or almost completely absent. As a result there are two types of area presenting very different conditions as regards illumination. Where the shrub-layer is well represented, the intensity of the diffuse light during the Light-Phase (cf. Part II, p. 92) ranges, according to the proximity of the stools, from 25 % to 72 % of the diffuse light-intensity in the open, the average being about 41·5 %. During the Shade-Phase this is reduced from about 1–11 %, with an average of nearly 4 % (cf. Table V).

TABLE V. *Light-intensities in Q. sessiliflora-Carpinus woods*

Wood	Character of Vegetation	Light-Phase %	Average of Light-Phase %	Shade-Phase %
Sherrard's	Dense shrub-layer, sparse ground-flora, chiefly Mosses and Fungi	33–50	40	4–11
Brock's		25–43	34·3	4·1–4·3
Symond's		33–46	38	1·3–4·0
Wormley		30·2		
Broxbourne		38·0		
Cox's	(<i>Q. sess.</i> + <i>Q. robur</i>) „ „			0·9–1·9
Sherrard's	Shrub-layer sparse or ab- sent, <i>Pteris</i> dominant	50–90	70	11–20
Symond's		66–90	70	—
Sherrard's		40–72	59	10–27
Brock's	Shrub-layer sparse or ab- sent, <i>Rubus fruticosus</i> dominant	50–55	50	—
Symond's		50–83	66·4	—
Titnol's		58–66	62	—
Wormley		—	—	16·6
Sherrard's	Shrub-layer sparse, <i>Rubus</i> and <i>Pteris</i> dominant	66–70	66	—
Symond's		73–80	76	—
Sherrard's	Sparse shrub-layer, <i>Nepeta</i> dominant	38–72	50	5–1·1
Sherrard's	Sparse shrub-layer, <i>Scilla</i> dominant	—	48	2·5
Sherrard's	<i>Mercurialis perennis</i> domi- nant	33–72	44·5	4·3–0·5
Symond's		33–43	38·6	4
Sherrard's	<i>Ficaria verna</i> dominant	40–60	54	1–0·1
Sherrard's	Path Society	50 upwards	—	13–20
Symond's		50 upwards	—	5·4–16
Wormley		—	—	8·3–21
Total range	(shrub-layer present)	25–72		0·9–11
Average	„ „ „	39·7		3·9
Total range	(shrub-layer sparse or abs.)	33–90		4·3–27
Average	„ „ „	66·6		13

In regard to these areas the low intensity during the Light-Phase is a noteworthy feature. Compared with the corresponding period in the *Q. robur-Carpinus* woods, the average intensity here, under coppice of similar age, is about 2 % to 10 % less (Salisbury, Part II, p. 93). This feature must be attributed to the fact that although the shrub-layer is scarcely ever as dense as in the *Q. robur* woods, the tree-canopy in these woods is much less open, and the more or less horizontally directed branches of the Oaks have a greater shading effect than the almost vertical branches of the coppice stools.

On the other hand we find that during the Shade-Phase the illumination beneath the shrub-layer is considerably higher than in the *Q. robur-Carpinus* woods. Now even where the shrub-layer in the latter is dense there is usually a considerable ground-flora, whilst in these woods the presence of a considerable shrub-layer is almost invariably associated with an almost complete absence of ground-vegetation. As the writer has already pointed out for the *Q. robur* woods with undergrowth (Part II, p. 97), it is the intensity during the Light-Phase combined with the time-factor which determines the amount of the ground-flora. Here in these woods as we have seen the conditions of illumination where there is a shrub-layer are altogether unfavourable to the ground-flora. For not only is the Light-Phase intensity low, but, since the shading effect is largely due to the tree-layer, there is no frequently recurring periodic impetus (cf. Part II, p. 98).

Whilst however the diminished light probably plays a very large part in bringing about a sparse vegetation, other factors, such as acidity, texture of soil, and water-supply are probably also involved.

The only species apart from Cryptogams which occur in these woods, where the Light-Phase intensity is very low, are extreme vernal forms such as *Adoxa moschatellina* and *Ficaria verna*. *Mercurialis perennis* also occurs in rather less shaded situations where the shrub-layer is fairly well developed.

Turning now to those areas where the Hornbeam is absent, or only represented by sparsely scattered stools, we find that the illumination both during the spring and summer is very much higher. Thus, during the Light-Phase the intensity ranges from 33 % to 90 %, with an average of over 66 %, whilst during the Shade-Phase the intensity does not fall below 4 % and may be as much as 27.2 %, with an average of 13 %.

Such considerable illumination during the Shade-Phase, though low in comparison with that in the open, enables shade-enduring species with aestival foliage to become dominant constituents of the ground-flora. Hence we find that areas where the Hornbeam is absent or scanty are often occupied by dense societies of Bramble or Bracken, whilst Honeysuckle, *Holcus mollis*, *Luzula pilosa*; and Wood Sage are by no means infrequent. All these are species which develop their new foliage relatively late in the year, but can tolerate a considerable degree of shading.

The Ground Ivy is locally abundant in some of these woods, and can survive a lower intensity than most species which retain their foliage throughout the summer. This is perhaps an outcome of the fact that though its new foliage is not produced till March or April yet the old foliage is frequently in large part retained throughout the autumn and winter, so that full advantage is taken of the Light-Phase.

The presence of abundant aestival species necessarily involves a quantitative diminution of those vernal species that might otherwise occupy the

better-lighted regions. Also the increased illumination results in a flora which though poor in quantity is numerically rich in species.

(4) The Phanerogamic Flora

If we disregard introductions and the numerous species of *Rubus*, etc., a total of 269 species of vascular plants have been observed in these woods, and of this number 48 represent trees, shrubs, and undershrubs, and the remaining 221 are herbs. From the *Q. sessiliflora* woods of Derbyshire, Moss (*loc. cit.*) has enumerated 231 vascular plants, exclusive of introduced species, but here as there it must be noted that owing to the sparsity of individuals the number of species is no measure of the amount of vegetation. Indeed the herbaceous carpet of the *Q. robur-Carpinus* woods is much more dense, although the Phanerogamic flora comprises only 265 species, of which 31 are confined to woods where *Q. sessiliflora* is also present. Two small woods of the *Q. sessiliflora-Carpinus* type in the neighbourhood of Hampstead, namely Bishop's Wood and Turner's Wood, have been briefly described by Tansley ("Hampstead Heath, its Geology and Nat. Hist.," *Vegetation*, pp. 85-111, London 1913). Comparison with those here described shows a general agreement in the character of tree- and shrub-layers. But as the list there given is based on "hasty visits during August and September" only, the marked discrepancies, both as to species and frequencies, in the ground-flora are perhaps more apparent than real. According to Mr Tansley, none of the herbaceous species appears to be at all abundant, except the Bracken and *Holcus mollis*, both of which are common in our woods. Mr Whitton however in the same work (p. 169) states that *Scilla nutans* is very abundant in Bishop's Wood, a feature which is of interest in connection with the local occurrence of a society dominated by this species in Sherrard's Wood.

(a) *The Tree-layer.* The dominant tree is *Quercus sessiliflora*, Salisb., but the hybrid Oak and *Q. robur* may be present in considerable amount. The average number of trees to the acre is usually higher than in the *Q. robur* woods (cf. Fig. 1). Seldom much below 30, the number may attain to over 70, and never have we found the trees sparsely scattered over large areas as is so frequently the case in woods where the common Oak predominates. This difference is probably to be attributed in part to better forestry, associated with the larger size of the woods of this type, but it may also be due to the more open texture of the soil and the increased illumination which tend to favour germination (cf. Boerker, R. H., *Ecological investigations upon the germination and early growth of Forest Trees*, Lincoln, Nebraska, 1916). In general it may be said that seedlings of both trees and shrubs are of greater frequency here than in *Q. robur-Carpinus* woods, and this in spite of the greater prevalence of rabbits. In these woods the Hornbeam occurs frequently as a tree and its seedlings are by no means uncommon. The great rarity of Hornbeam seedlings in the *Q. robur* woods is probably largely due to the fact that some years must

elapse before a coppiced stool bears fruit and often this does not take place until it is again cut. Here however the frequent Hornbeam trees supply the requisite seed.

The most important of the associated trees is unquestionably *Betula pubescens*, Ehrh., with which is occasionally associated *B. alba*, L., but never

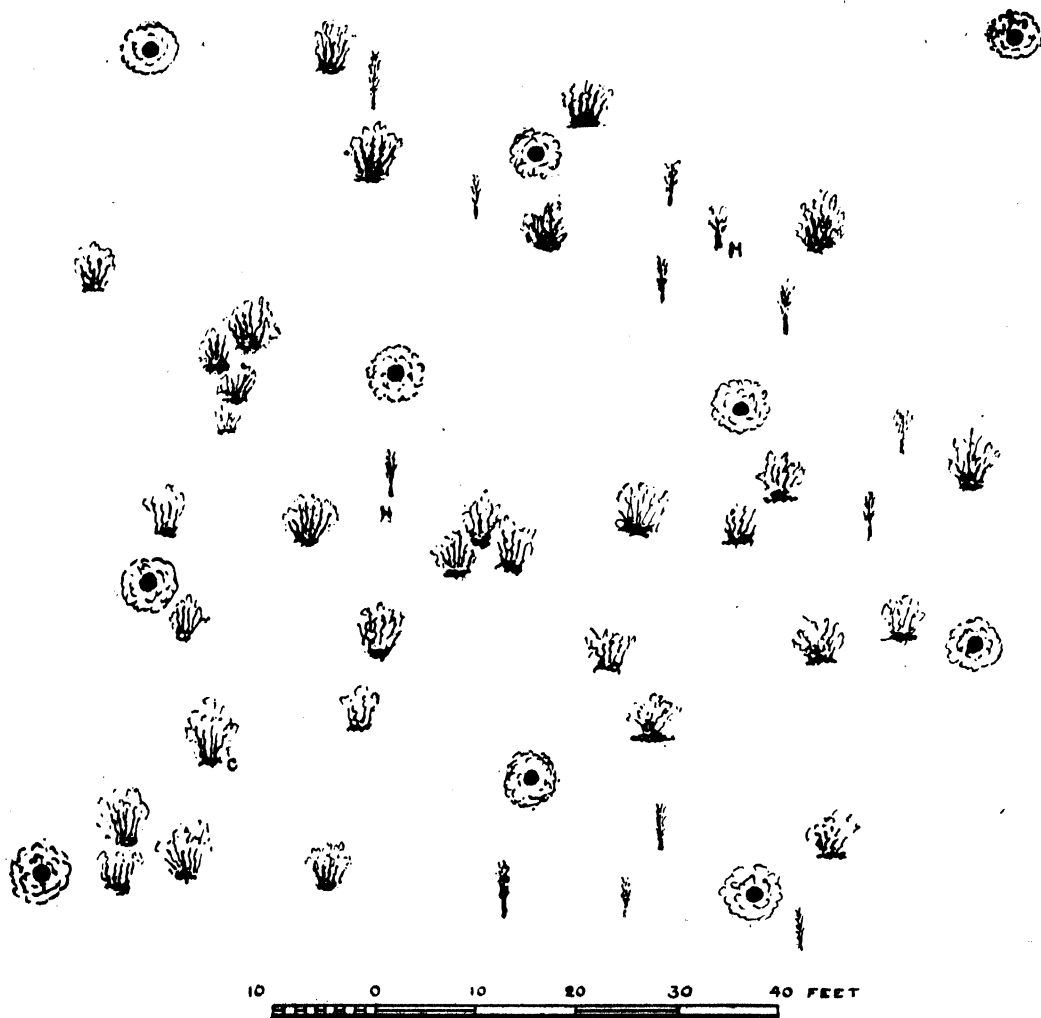


FIG. 1. Chart of a typical portion of Sherrard's Park Wood, showing the standard oaks (*Q. sessiliflora*) more numerous than the oaks in *Q. robur* woods, the hornbeam stools (C) and the hornbeam saplings (H).

in such quantity. The Birch rapidly colonises areas adjacent to the main woods, but owing to human interference no very advanced stage is usually reached. *Pyrus aucuparia*, Gaertn., though usually rare, is very characteristic as it is also of the *Q. sessiliflora* woods elsewhere, and the same may be said of *Ilex aquifolium*, L., *Alnus glutinosa*, Gaertn., *Pyrus torminalis*, Ehrh., and *P. malus*, L. These are all very rare, but are apparently confined to woods

of this type or *Q. robur* woods in which *Q. sessiliflora* is also present and which are consequently open to suspicion of having been planted. The Aspen is occasional in its distribution, and both the smooth and hairy leaved varieties occur, the latter being sometimes frequent. *Prunus avium*, L., *Ulmus montana*, Sm., and *Fraxinus excelsior*, L., are all trees that occur with considerable frequency in the Oak-Hazel woods, but are generally less common in the *Q. robur-Carpinus* woods. Here these trees are more or less restricted to the hollows and lower slopes of the valleys where the water-content is higher, the soil consists of finer particles, and is richer in mineral salts. In these situations too *Q. robur* may in part replace *Q. sessiliflora*. Both the soil-conditions and the vegetation in these hollows approximate very closely to those in the *Q. robur-Carpinus* woods of the stiffer loams, and it may be significant that the amount of mineral salts, as measured by the electrical conductivities of the soil-solutions, in these situations corresponds with that of the soil-solution from the *Q. robur-Carpinus* woods. There are two woods where the Ash is locally abundant, namely Titnol's Wood and a part of Wormley Wood. They illustrate the two extremes under which the Ash is found (cf. Moss, *Veget. of Peak Distr.*, p. 69). The former locality is relatively dry, and the latter exceptionally wet. As however Titnol's Wood exhibits a lower acidity than any of the other woods of this type we may perhaps here possess a clue to the prevalence of this species (cf. Part II, p. 99).

Several Conifers occur, but none is indigenous. Those most commonly planted are the Spruce, the Larch, and the Douglas Fir, less frequently the Scotch Pine.

(b) *The Shrub-layer.* Here, as in the *Q. robur-Carpinus* woods, the shrub-layer is chiefly composed of *Carpinus betulus*, var. *provincialis*, Grenier et Godson. Both *Rubus fruticosus*, Agg. L., and *Lonicera periclymenum*, L., are very common and the former is locally dominant. The Hazel is frequent, but, like the Dogwood, Elder, Maple, and Blackthorn, is chiefly found where the surface approaches close to the chalk, especially in the damp hollows. Elder is particularly characteristic of the latter situations (cf. Part II, p. 99). Frequent members of the shrub-layer are *Crataegus monogyna*, Jacq., *C. oxyanthoides*, Thuill., and various species of Roses and Willows. Especially characteristic, although very rare, are *Rhamnus frangula*, L., and *Viburnum opulus*, L. The complete list is given in Table VI.

Associated with the more complete arboreal canopy the Hornbeam never attains to the density exhibited in the *Q. robur* woods. But where the shrub-layer proper is present the combined shading effect of trees and coppice is sufficient to restrict the ground-vegetation almost entirely to Mosses and Fungi. As previously stated however there are considerable areas from which the Hornbeam and other shrubs proper are almost completely absent. These areas are often covered by a dense straggling growth of Brambles. Hence we can recognise two distinct societies in the shrub-layer, namely that in which

TABLE VI. *List of trees and shrubs**Trees:*

<i>Quercus sessiliflora</i> , Salish.	dom.
„ <i>robur</i> , L.	r-c
<i>Q. robur</i> × <i>Q. sessiliflora</i> , Mocek	o-f
<i>Abies excelsa</i> , DC.	planted
<i>Acer pseudoplatanus</i> , L.	vr
<i>Alnus glutinosa</i> , Gaertn.	r-vr
<i>Betula alba</i> , L.	o-f
„ <i>pubescens</i> , Ehrh.	f-c
<i>Carpinus betulus</i> , var. <i>provincialis</i> , Grenier et Godron	f
<i>Castanea sativa</i> , Mill.	planted (?), rare
<i>Fagus sylvatica</i> , L.	vr-f
<i>Fraxinus excelsior</i> , L.	o-lc (damp places, or if dry less acid)
<i>Ilex aquifolium</i> , L.	r-lf
<i>Larix decidua</i> , Mill.	planted, f
<i>Pinus sylvestris</i> , L.	planted, f
<i>Populus alba</i> , L.	r
„ <i>tremula</i> , L.	o-f
„ „ „ var. <i>glabra</i> , Syme.	o-lf
„ „ „ var. <i>sericea</i> , Doll.	o-f
<i>Prunus avium</i> , L.	r-l
<i>Pseudotsuga douglasii</i> , Carr.	planted, f (2)
<i>Pyrus aucuparia</i> , Gaertn.	o
„ <i>communis</i> , L.	r (2)
„ <i>malus</i> , var. <i>mitis</i> , Wallr.	r-vr
„ <i>tormentalis</i> , Ehrh.	vr
<i>Ulmus montana</i> , Sm.	r-lf

Shrubs and undershrubs:

<i>Acer campestres</i> , L.	o
<i>Calluna vulgaris</i> , Salish.	lc (3)
<i>Carpinus betulus</i> , var. <i>provincialis</i> , G. and G.	sd
<i>Clematis vitalba</i> , L.	chalk-pits only
<i>Cornus sanguinea</i> , L.	rr-o, near chalk or damp places
<i>Corylus avellana</i> , L.	f (lc in damper hollows)
<i>Crataegus monogyna</i> , Jacq.	f
„ <i>oxycanthoides</i> , Thuill.	f
<i>Hedera helix</i> , L.	f
<i>Lonicera periclymenum</i> , L.	c-ab
<i>Prunus spinosa</i> , L.	f-lc, especially near chalk
„ <i>institia</i> , L.	rr (1)
<i>Rhamnus catharticus</i> , L.	vr (2), near chalk
„ <i>frangula</i> , L.	vr
<i>Rhododendron ponticum</i> , L.	r-lf, planted
<i>Ribes rubrum</i> , L.	vr (1)
<i>Rosa arvensis</i> , Huds.	f (near edge)
„ <i>canina</i> , L.	f (near edge)
„ <i>stylosa</i> , Desv.	r (1)
„ <i>tomentella</i> , Leman	r (1)
„ <i>tomentosa</i> , Sm.	r (1)
<i>Rubus fruticosus</i> , L. (agg.)	c-ab
(Incl. <i>R. koehleri</i> , Weihe, <i>R. rhamnifolius</i> , Weihe and Nees, <i>R. leucostachys</i> , Schleich, etc.)	
<i>Rubus idaeus</i> , L.	r-f
<i>Ruscus aculeatus</i> , L.	vr (1)
<i>Salix aurita</i> , L.	f-r
„ <i>caprea</i> , L.	f-r
„ <i>cinerea</i> , L.	f-r
<i>Sambucus nigra</i> , L.	r-lc (in damp chalky depressions)
<i>Solanum dulcamara</i> , L.	f, edge
<i>Viburnum opulus</i> , L.	vr

The symbols employed are as follows: d, dominant; sd, sub-dominant; ab, abundant; vc, very common; c, common; fc, fairly common; f, frequent; o, occasional; rr, rather rare; r, rare; vr, very rare; l, local. A number in brackets indicates the number of woods in which the species has been observed when not of general occurrence.

the Hornbeam is present as the dominant and that in which the Bramble is dominant.

The Rubus fruticosus society. A study of the water-content, humus-content, mechanical structure, and light-intensity of the soils of the areas dominated by *Rubus fruticosus* (cf. Tables II, III, IV, and V) indicates a wide range of conditions. Thus whilst the average water-content is about 28.5 % different localities, even during the winter-months, show a variation of between 23 % and 38 %. The organic material too ranges in amount from 5.46 % to 12.2 %. Evidently then the *Rubus* society is not related to any very restricted edaphic conditions and we must seek an explanation for its dominance in other causes. The *Rubus* society often occupies large areas and the dominant species is accompanied by Honeysuckle, sometimes in considerable quantity, and Bracken which is often common. Other frequent species are *Holcus mollis*, *Anemone nemorosa*, and *Oxalis acetosella*. But with these exceptions shrubs and herbs are alike rare. A careful examination of these areas will however often reveal the remains of old stools, in various stages of decay, that bear evidence to the presence here of a shrub-layer at no very distant date. An examination of coppiced or felled areas shows that in the first year after cutting Bramble seedlings appear in large numbers. In the normal course of development these grow for several years, but ultimately die as they become choked out by the shade effect of the sprouting stools. There can be little doubt that the influencing factor to bring about the establishment of the permanent *Rubus* society is the failure of the coppice to develop vigorous shoots, a failure that is brought about mainly by the rabbits which abound on these light soils, and which nibble the young shoots as they develop. Owing no doubt to the armature of prickles, the Bramble seedlings appear to be immune from the depredations of these animals.

Comparison of the light intensities here and in the *Pteris* society (cf. Table V) shows that most of the areas occupied by *Rubus* would in this respect be equally suitable for the Bracken. But whereas the Phanerogam colonises with remarkable rapidity both by seeds and vegetative spread, the Cryptogam but seldom produces prothalli in these woods and its rate of expansion by rhizomes is slower. Both have summer foliage which begins to develop towards the end of May, but can endure a diminution of the light during the Shade-Phase to about 10 %. Owing to the controlling influence of light occupation in a woodland is often a decisive factor, since the late comer has to combat the shade of its competitor as well as that cast by the trees and shrubs. The fact that *Pteris* and *Rubus* do sometimes occur together in the relation of co-dominants bears testimony to the remarkable capacity of the Bracken for waging this unequal warfare. It is however doubtful whether even this species is capable of making headway once the complete dominance of the other has become established. Probably *Pteris* has the advantage in drier situations, whilst *Rubus fruticosus* flourishes best where the soil is

naturally damper. This point is brought out by a comparison of the mechanical analyses (see Table II) from which it will be seen that in the same wood, although the composition of the soil from the two societies is similar, the proportion of fine particles is greater where the Bramble predominates. Finally we may note that although the two societies overlap to a considerable extent, the *Rubus* society extends into deeper shade, both as regards Light and Shade-Phases, than the Bracken society.

(c) *The Ground-flora*. The herbaceous vegetation is strikingly scanty, although embracing a comparatively large number of species. Except locally where the water-content is high (cf. *infra*), the continuous sheets of Wood Anemone, Hyacinth, Dog's Mercury, etc., which are such a feature on the Clay-with-flints, are conspicuously absent. We can however recognise several ground societies, dominated respectively by Bracken, Dog's Mercury, Ground Ivy, Lesser Celandine, and Hyacinth. From the viewpoint of area occupied the first is by far the most important and the three last comparatively insignificant. Here indeed, as in *Q. sessiliflora* woods elsewhere, the continuous sheets of Bracken fronds are the most salient feature. In only one wood, namely Wormley, does the Anemone become locally abundant, whilst typically it is rather rare. A complete list of the shade species is given in Table VII, and it will be seen that comparatively few species attain any degree of frequency, and this is usually of a purely local character. Apart from such species, which become important under special conditions, the more generally distributed are *Anemone nemorosa*, *Epilobium montanum*, *Holcus mollis*, *Luzula pilosa*, *Oxalis acetosella*, *Primula acaulis*, *Teucrium scorodonia*, *Viola sylvestris*, and the ubiquitous Bracken.

The Pteris society. This is the best represented society in the *Q. sessiliflora*-*Carpinus* woods, and often covers extensive areas. It is equivalent to the Mesopteridetum of Woodhead ("Ecology of Woodland Plants in the neighbourhood of Huddersfield," *Journ. Linn. Soc.*, vol. xxxvii, 1906; cf. also Wilson, *loc. cit.*, p. 886). Like the *Pteris* society, so characteristic of the *Q. sessiliflora* woods in Yorkshire, Somerset and Wales, it is poor in species, doubtless due largely to the shading effect of the Bracken. In summer the light beneath its foliage is under 8 % of the diffuse light intensity outside. Even the vernal species do not flourish here, as they are unable to benefit greatly by the Light-Phase owing to the persistence of the dead fronds. The latter are indeed probably as efficient a means of eliminating serious competitions as a rosette habit (cf. Lindman, *New Phytologist*, vol. xii, 1913). The Bracken society typically occurs where the shrub-layer is very sparse, the light intensity during the Light-Phase is from 50-90 %, and during the Shade-Phase is relatively high (cf. Table V). Woodhead (*loc. cit.*, p. 338) noted the same tendency of the Bracken to become abundant where the shrub-layer was sparse in the woods of the Huddersfield district. Here, as there, this condition has probably been brought about through the action of rabbits.

TABLE VII. *List of Species comprising the Shade-Flora*

<i>Adoxa moschatellina</i> , L. ...	lf (2) (Ficaria-soc.)
<i>Ajuga reptans</i> , L. ...	lf-le (Mercurialis-soc.)
<i>Anemone nemorosa</i> , L. ...	rr-le
<i>Arctium nemorosum</i> , Lej. ...	vr
<i>Arenaria trinervia</i> , L. ...	r
<i>Arum maculatum</i> , L. ...	o-le (Mercurialis- and Ficaria-soc.)
<i>Asperula odorata</i> , L. ...	rr-lf
<i>Athyrium filix-foemina</i> , Roth. ...	vr
<i>Blechnum spicant</i> , With. ...	l (2)
<i>Carex pendula</i> , Huds. ...	vr
„ <i>sylvatica</i> , Huds. ...	r
<i>Circaea lutetiana</i> , L. ...	r
<i>Conopodium denudatum</i> , Koch ...	r-rr
<i>Convallaria majalis</i> , L. ...	vr (3), probably extinct except in one
<i>Epilobium montanum</i> , L. ...	o
<i>Epipactis violacea</i> , Bor. ...	r
<i>Equisetum maximum</i> , Lamk. ...	l (2)
„ „ var. <i>serotinum</i> , Braun ...	(1)
<i>Euphorbia amygdaloides</i> , L. ...	rr (lf, 1)
<i>Ficaria verna</i> , DC. ...	r-le
<i>Fragaria vesca</i> , L. ...	cr
<i>Galeobdolon luteum</i> , Huds. ...	rr-f
<i>Geum urbanum</i> , L. ...	vr
<i>Holcus mollis</i> , L. ...	c-r
<i>Listera ovata</i> , Br. ...	rr
<i>Luzula maxima</i> , DC. ...	r-f (3)
„ <i>pilosa</i> , Willd. ...	o-f
<i>Lycopodium clavatum</i> , L. ...	(Broxbourne, 1855, now extinct)
<i>Mercurialis perennis</i> , L. ...	l. ab-rr
<i>Narcissus pseudo-narcissus</i> , L. ...	lr (1)
<i>Neottia nidus-avis</i> , L. ...	vr (1)
<i>Nepeta glechoma</i> , Benth. ...	o-l. ab
<i>Nephrodium dilatatum</i> , Desv. ...	vr (1)
„ <i>filix-mas</i> , Rich. ...	rr- vr
„ <i>montanum</i> , Baker ...	vr (2)
„ <i>spinulosum</i> , Desv. ...	vr (1)
<i>Orchis mascula</i> , L. ...	r
<i>Oxalis acetosella</i> , L. ...	o-f
<i>Paris quadrifolia</i> , L. ...	r (2)
<i>Primula acaulis</i> , L. ...	r-f
<i>Pteris aquilina</i> , L. ...	rc-l. ab
<i>Ranunculus auricomus</i> , L. ...	lr, damper parts
<i>Rumex condyloides</i> , Biberstein ...	r-lf
<i>Sanicula europaea</i> , L. ...	rr-f (Mercurialis- and Ficaria-soc.)
<i>Scilla nutans</i> , Sm. ...	rr (la, 1)
<i>Serophularia nodosa</i> , L. ...	vr
<i>Sedum telephium</i> , L. ...	r (1)
<i>Teucrium scorodonia</i> , L. ...	o-f
<i>Veronica montana</i> , L. ...	rr
<i>Viola riviniana</i> , Reichb. ...	r-f
„ „ „ f. <i>nemorosa</i> , Neuman ...	r
„ <i>sylvestris</i> , Kitt. ...	r-o
„ „ „ var. <i>punctata</i> , Greg. ...	r-fc

It is probable that the Ferns were formerly more abundant and more generally distributed than at present.

Except where the Bracken only occurs as scattered individuals, the light intensity during the Shade-Phase does not fall below 11 % (cf. Table V), but occasional plants are met with at intensities of as low as 4.1 %. This harmonises with the minimum illumination which Wiesner gives for this plant, namely $L = 1/60$, a value which corresponds to about 5 % of maximum diffuse illumination (Wiesner, J., *Lichtgenuss d. Pflanzen*, p. 165, Leipzig, 1907).

The distribution of the Bracken in these woods corresponds then with that observed by Woodhead and is doubtless correlated with the late development of the assimilatory organs which begin to appear above the ground at about the inception of the Shade-Phase (i.e. middle of May).

The *Pteris* society usually exhibits a natural water-content of about 28.5 % though even in summer this may be as high as 45 % and in winter as low as 25 % (cf. Table IV). But it must be noted that the soil of this society exhibits an unusually high organic content (cf. Table III), ranging from 5.00 % to 15.76 % (average 9.92 %). The accumulation of peat in the upper layers of the soil produced by the Bracken itself may reach a depth of from 5 to 6 in. To this is almost entirely due the large water-content and its extreme variability. That this is the case is shown by the mechanical analyses (cf. Table II) from which it is clear that the *Pteris* society is characteristic of soil with a smaller proportion of silt and clay than in any other society except that dominated by *Scilla nutans*. In the latter, however, *Pteris aquilina* is also common. Here then as in the *Q. robur* woods it may be said that the Bracken occupies areas which, either owing to their configuration or the organic constitution of the soil, are naturally dry and acid. (Acidity .42-.52, Acidity-humus ratio 1:8.8-1:14.1.)

The more characteristic associates of the Bracken are *Rubus fruticosus*, agg. (c), *Lonicera periclymenum* (f-vc), *Teucrium scorodonia* (lf), *Scilla nutans* (lf-r), *Anemone nemorosa* (r-f), and *Holcus mollis* (c), the last-named species in the better-lighted parts.

The Scilla nutans society. This society which is probably to be regarded as a sub-society of that dominated by Bracken occupies one or two very limited areas in Sherrard's Wood, where the soil is derived from the Reading Beds and contains a very high proportion of pebbles. It is particularly rich in coarse particles and deficient in silt and clay (cf. Table II). In addition the humus and water-content are especially low. The *Scilla* society is probably a local variant of the *Pteris* society in which the comparative scarcity of Bracken and abundance of the vernal species are largely the effect of a diminished light-intensity during the Shade-Phase (cf. Table V). The only conspicuous accompanying species, apart from the Bracken, are *Holcus mollis* and *Galeobdolon luteum*. The extremely pebbly character of the soil here is the more surprising in view of Wilson's observations (*loc. cit.*, p. 894) that *Scilla nutans* was absent from very pebbly areas.

The Nepeta glechoma society. Like the preceding this is of local occurrence in Sherrard's Wood and one other. In the former area however several acres are occupied by an unprecedented growth of the Ground Ivy, with which are associated the Dog's Mercury (fc), and the Bugle (f-rr). The soil exhibits a slightly higher humus-content (about 7 %), and a larger proportion of silt and clay than in the *Scilla* society. The low summer water-content is to be attributed to the topographical position of this society. The light-intensity

during the Shade-Phase is probably too low to permit of the growth of Braeken, but nevertheless sufficiently high to admit of an ombrophilous species with persistent foliage becoming dominant.

The Mercurialis society. As in the *Q. robur-Carpinus* woods this society is restricted to situations that are either damp or, when relatively dry, where the soil covering the chalk is shallow. Typically the slopes of the depressions and valleys in these woods are almost always occupied by this society (cf. Fig. 1) which merges below into that dominated by *Ficaria verna*. The light-intensity is low, exhibiting an average of about 42 % during the Light-Phase and of about 4 % during the Shade-Phase. The humus-content of the soil varies between 6.32 % and 19.4 % (cf. Table III), but as a rule is distinctly lower than where the Braeken predominates. The mechanical analysis (see Table II) also indicates that the high water-content here, av. 31 %, is largely an outcome of the physical structure of the soil; thus in Brock's Wood the

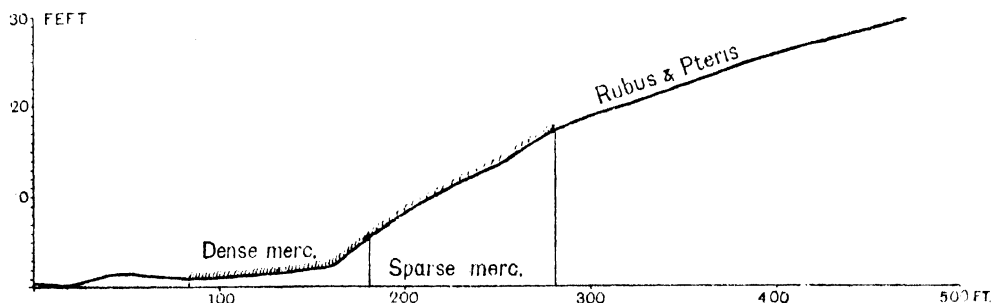


FIG. 2. Profile, Brock's Wood. Showing the occurrence of *Rubus* and *Pteris* on the high ground and *Mercurialis* in the valley. Surveyed by A. H. Salisbury, M.S.A.

Mercurialis society has a soil with an average of 38.24 % of silt and clay, whilst the adjoining *Pteris* society has only 17.76 %. In Titnol's Wood the water-content in this society was only 27.4 %, as compared with 53.4 % in Symond's Hyde Wood on the same day. But this low water-content is associated with a low acidity which even after coppicing only amounts to 0.3 %. The facts of distribution here then confirm the view expressed (Part II, p. 104), that the occurrence of *Mercurialis perennis* is mainly conditioned by the low acidity of the soil-solution (·31). However, low acidity is often associated with a higher mineral content, a factor that may also play its part in the determination of distribution.

Common associates of the Dog's Mercury are the Bugle and the Ground Ivy. In addition Wood Sorrel, Yellow Deadnettle, Strawberry, Wood Violet, Primrose, Enchanter's Nightshade, Wood Sanicle, and *Veronica montana* are sometimes frequent. *Sanicula europaea* and *Fragaria vesca* are particularly met with in this society when the soil above the chalk is shallow.

The Ficaria verna society. Damp hollows and the floors of the valleys where the shade in the summer is considerable and, owing to the topographical

relations, the soil is always damp in spring, are generally occupied by a society in which the dominant species is *Ficaria verna*. Where the illumination during the Shade-Phase is higher *Mercurialis perennis* becomes frequent and the two societies merge almost imperceptibly the one into the other. As in the *Q. robur* woods, *Arum maculatum* is a frequent associate of *Ficaria*, whilst *Ranunculus auricomus* is confined to this society, though of rare occurrence. The acidity is even lower than in the last society (cf. Table IV).

A sub-society is encountered in two of these woods where there are damp hollows with but a shallow soil in close proximity to the chalk (acidity nil). These are characterised by the frequency or even co-dominance of *Adoxa moschatellina* (cf. Part II, p. 104). Very common constituents of this society are various Hypnaceous Mosses, particularly the unattached form of *Eurhynchium praelongum*, whilst in one wood *Porotrichum alopecurum* is frequent. The light-intensity is about the same as that of the *Mercurialis* society during the Light-Phase, but during the Shade-Phase is somewhat lower.

The Path society. The considerable illumination (cf. Table V) of the paths which even during the Shade-Phase ranges from over 5 % to as much as 21 % (or under exceptional conditions even higher) enables but slightly ombrophilous species to compete here with the more specialised woodland types. Partly as a consequence of this and partly owing to the high water-content and low acidity we find a flora not merely rich in individuals, but comprising more than 80 species. The paths and rides in these woods are very wet in winter and moist even in summer. The humus-content is not particularly high, 7.44—10.7 %, but the percentage of silt and clay is large and comparable to that of the *Q. robur*-*Carpinus* woods (cf. Table III). Usually the path exhibits a higher water-content than any of the other societies, with an average of about 35.6 %. Associated with this fact and the frequent inundation of the paths in autumn we find that the two most characteristic species are the land-form of *Callitriche stagnalis* (vc-f) and *Polygonum hydropiper* (fc-l. ab). The other important species are damp-loving plants, of which may be mentioned *Nepeta glechoma* (fc-vc), *Prunella vulgaris* (c), *Poa annua* (f-l. ab), *Fragaria vesca* (f-c), *Gnaphalium uliginosum* (f-fc), *Galium palustre* (f-c), *Lysimachia nemorum* (c-vc), *Geum urbanum* (c), *Mentha arvensis* (o-c), *Ranunculus repens* (o-c), *Circaea lutetiana* (f-lc), *Juncus bufonius* (lf-fc), *Ajuga reptans* (f-c), *Stellaria uliginosa* (f), *Peplis portula* (lf-c), *Oxalis acetosella* (f-l. vc), and *Mercurialis perennis* (f). In the woods on the London Clay *Cardamine flexuosa* is also a prominent constituent of this society. The presence of both the Enchanter's Nightshade and the Dog's Mercury can be related to the low acidity, and we may remark that many of the more abundant species of the *Q. robur* woods are here almost confined to the path society. It is interesting to note that where these damp paths and rides are deeply shaded there is a carpet of vegetation dominated by Crypto-

gams, especially Mosses. This condition recalls the dominant Cryptogamic flora in the deep shade of many of the wet steep-side valleys of Yorkshire, Somerset, and Wales, occupied by woods of *Q. sessiliflora* (cf. Moss, in *Types of British Vegetation*, p. 138; Salisbury, *Proc. Linn. Soc., loc. cit.*).

Very locally a dry type of path is located where the soil is gravelly and where the vegetation is comparable to that of a gravel heath. The characteristic species of such situations are *Veronica officinalis*, *Galium saxatile*, *Alchemilla arvensis*, *Hypericum humifusum*, and *Rumex acetosella*. This is such a definite type of vegetation that it may be convenient to designate it by the name of the *Alchemilla arvensis* society, since that species is the most symptomatic of these special conditions. It may here be noted that the particular form of *Alchemilla arvensis* is that found on gravel heaths and is usually an erect and often but little branched plant.

The Anemone society. This society only occurs in the woods of this type on the London Clay and there it is strictly local.

TABLE VIII. *Path and Marginal Species and Coppiced Flora*

Species	Margin of woods and rides	Path	Coppiced Areas
<i>Aegopodium podagraria</i> , L. ...	l	—	—
<i>Agrimonia eupatorium</i> , L. ...	r	—	r
<i>Agrostis alba</i> , L. ...	f-vc	—	f-c
„ <i>canina</i> , L. ...	—	—	rr
„ <i>vulgaris</i> , With. ...	—	—	r
<i>Aira caespitosa</i> , L. ...	lf	vr	—
„ <i>flexuosa</i> , L. ...	r	—	—
<i>Ajuga reptans</i> , L. ...	f	f-c	f-c
<i>Alchemilla arvensis</i> , Scop. ...	—	l (drier parts)	—
„ <i>vulgaris</i> , L. ...	—	o	—
<i>Anagallis arvensis</i> , L. ...	—	—	o (1)
<i>Anemone nemorosa</i> , L. ...	o	—	—
<i>Angelica sylvestris</i> , L. ...	r-f (3)	—	—
<i>Anthoxanthum odoratum</i> , L. ...	—	o	f-vc
„ „ <i>var. villosum</i> , Lois. ...	o	o	o-lf
<i>Anthriscus sylvestris</i> , Hoffm. ...	f	—	—
<i>Aquilegia vulgaris</i> , L. ...	r (2), now apparently extinct	—	—
<i>Aretium nemorosum</i> , Lej.	f-rr	—	o-f
<i>Arenaria serpyllifolia</i> , L. ...	—	—	r (1)
„ <i>trinervia</i> , L. ...	o	r	f-c
<i>Arrhenatherum avenaceum</i> , Beauv. ...	o	—	—
<i>Arum maculatum</i> , L. ...	lf	—	o
<i>Asperula odorata</i> , L. ...	c-f	r-rr	r-f
<i>Atropa belladonna</i> , L. ...	vr (1)	—	—
<i>Barbarea vulgaris</i> , Br. ...	—	—	rr
„ „ <i>var. arcuata</i> , Reichb. ...	—	—	r (1)
<i>Bellis perennis</i> , L. ...	—	r	—
<i>Brachypodium sylvaticum</i> , R. and S. ...	lf-f	—	—
<i>Bryonia dioica</i> , Jacq. ...	o	—	—
<i>Calamintha clinopodium</i> , Benth. ...	f	f	—
<i>Calamagrostis epigeios</i> , Roth. ...	rr (3)	—	—
<i>Callitriche stagnalis</i> , Scop. ...	—	vc-f	l
<i>Campanula latifolia</i> , L., f. <i>alba</i> ...	vr (1)	—	—
<i>Cardamine flexuosa</i> , With. ...	f	f (on London Clay)	—
„ „ <i>pratensis</i> , L. ...	—	—	vr (1)
<i>Carex binervis</i> , Sm. ...	r (2)	—	—
„ <i>divulsa</i> , Good. ...	r (2)	—	—
„ <i>glauca</i> , Scop. ...	l (1)	—	—

TABLE VIII (continued)

Species	Margin of woods and rides	Path	Coppiced Areas
<i>Carex lepidocarpa</i> , Tausch	... 1 (1)	—	—
„ <i>leporina</i> , L.	... lf (1)	—	—
„ <i>pallescens</i> , L.	... o-lc	—	r-f
„ <i>pendula</i> , Huds.	... lf-f	1 (specially on London Clay	—
„ <i>pilulifera</i> , L.	... o	—	o
„ <i>pseudo-cyperus</i> , L.	... r (2)	—	—
„ <i>remota</i> , L.	... o (1)	—	—
„ <i>strigosa</i> , Huds.	... r (on lighter soils)	—	—
„ <i>sylvatica</i> , Huds.	... o-rr	—	—
„ <i>vesicaria</i> , L.	... r (3)	—	—
„ <i>vulgaris</i> , Fries	... vr (1)	—	—
<i>Cerastium glomeratum</i> , Thuill.	... —	o (drier parts)	—
„ <i>vulgatum</i> , Fries	... —	r-f	r-vr
<i>Chaerophyllum temulum</i> , L.	... f	—	—
<i>Chrysosplenium oppositifolium</i> , L.	... lf (2) (by stream)	—	—
<i>Cicuta virosa</i> , L.	... lr (1)	—	—
<i>Circaea lutetiana</i> , L.	... o-lf	r-lc	r-rr (damp spots)
<i>Cnicus lanceolatus</i> , Hoffm.	... r-o	—	—
„ <i>palustris</i> , Hoffm.	... o-c	—	f-l. ab.
<i>Conium maculatum</i> , L.	... —	—	vr (near chalk)
<i>Conopodium denudatum</i> , Koch	... r-f	—	rr
<i>Crepis virëns</i> , L.	... —	—	r
<i>Dactylis glomerata</i> , L.	... vr-f	—	—
<i>Digitalis purpurea</i> , L.	... r-lf (3)	—	l-c (3)
<i>Dipsacus sylvestris</i> , L.	... r	—	o
<i>Epilobium angustifolium</i> , L.	... r-f	—	o
„ <i>montanum</i> , L.	... f-c	r-f	r-c
„ <i>tetragonum</i> , L.	... r	r-o	r
„ <i>obscurum</i> , Schenk	... r	—	r
<i>Epipactis latifolia</i> , Sw.	... vr	—	—
„ <i>violacea</i> , Bor.	... r-vr	—	vr
<i>Erythraea centaureum</i> , Pers.	... —	r-f	f-vc
„ „ „ f. <i>alba</i>	... —	—	vr (1)
<i>Eupatorium cannabinum</i> , L.	... lf (2)	—	—
<i>Euphorbia amygdaloides</i> , L.	... rr-l	—	r-lc
<i>Euphrasia officinalis</i> , L.	... —	f-lf (2)	—
<i>Festuca gigantea</i> , Vill.	... lf (1) (damper spots)	—	—
„ <i>myurus</i> , L.	... —	—	o (1)
<i>Ficaria verna</i> , DC.	... r	r	—
<i>Fragaria vesca</i> , L.	... c-f	f-c	f-c
<i>Galeopsis tetrahit</i> , L.	... o (2)	—	o (2)
<i>Galeobdolon luteum</i> , Huds.	... f-lc	—	o-l. ab
<i>Galium aparine</i> , L.	... f	—	r
„ <i>mollugo</i> , L.	... o	—	—
„ <i>palustre</i> , L.	... —	f-c	o (damper spots)
„ <i>saxatile</i> , L.	... —	l-f (3) (dry parts)	—
<i>Genista tinctoria</i> , L.	... r-l (3)	—	—
<i>Geranium columbinum</i> , L.	... —	—	o (2)
„ <i>dissectum</i> , L.	... rr	—	r
„ <i>robertianum</i> , L.	... f	r	r
<i>Geum urbanum</i> , L.	... c-f	c	r-f
<i>Gnaphalium sylvaticum</i> , L.	... r (2)	—	r-lf (2)
„ <i>uliginosum</i> , L.	... f	f-fc	f
<i>Habenaria chlorantha</i> , Bab.	... —	—	r (3)
<i>Heraacleum spondylium</i> , o-f	—	r
„ <i>var. angustifolium</i> , Huds.	... r	—	—
<i>Hieraceum boreale</i> , Fries, agg.	... o-f	r	—
<i>Holcus lanatus</i> , L.	... f	r	f-vc
„ <i>mollis</i> , L.	... o-c	—	f-c
<i>Hypericum androsaemum</i> , L.	... vr	—	—
„ <i>hirsutum</i> , L.	... r (1)	—	—
„ <i>humifusum</i> , L.	... —	lf	f-c
„ <i>perforatum</i> , L.	... f	—	f-lf
„ <i>pulchrum</i> , L.	... —	o (drier parts)	o-r

TABLE VIII (continued)

Species	Margin of woods and rides	Path	Coppiced Areas
<i>Hypericum tetrapterum</i> , Fries	—	o-f	o-f (damper spots)
(<i>H. quadrangulum</i> , L. pro parte)	—	—	—
<i>Hypochaeris radicata</i> , L.	o	—	r
<i>Inula dysenterica</i> , Gaert.	l (1) (by stream)	—	—
<i>Juncus acutiflorus</i> , Ehrh.	—	l (2)	—
„ <i>bufonius</i> , L.	—	lf-fe	o
„ <i>conglomeratus</i> , L.	l. vc (1)	o	o-le
„ <i>effusus</i> , L.	—	l	lf
„ <i>supinus</i> , Moench	—	(2)	—
<i>Lactuca muralis</i> , Fresen.	r (2)	—	—
<i>Lapsana communis</i> , L.	rr	—	r
<i>Lathyrus macrorhizus</i> , Wium.	rr (3)	—	—
<i>Listera ovata</i> , Br.	—	vr (1)	—
<i>Lolium perenne</i> , L.	—	—	r (1)
<i>Lotus major</i> , Sm.	o-f	o	r
<i>Luzula maxima</i> , DC.	f-rr (3)	rr (3)	r-lf (3)
„ <i>multiflora</i> , Lej.	—	o	f-rr
„ „ „ var. <i>congesta</i> , Lej.	—	—	o-f
„ <i>pilosa</i> , Willd.	o-fe	o	o-fe
<i>Lychnis flos-cuculi</i> , L.	—	l	l-f (damp spots)
„ <i>vespertina</i> , Sibth.	r (1)	—	r (1)
<i>Lysimachia nemorum</i> , L.	—	c-vc	c-ab
„ <i>nummularia</i> , L.	—	o (?)	—
<i>Malva moschata</i> , L.	r	—	—
<i>Melampyrum pratense</i> , L.	o-f (1)	—	f
<i>Melica uniflora</i> , Retz.	lf-fe	r	—
<i>Mentha arvensis</i> , L.	r	o-c	o (damp spots)
„ <i>pubescens</i> , Willd.	f (1, damp places)	—	—
„ <i>sativa</i> , L.	r (2)	—	—
<i>Menyanthes trifoliata</i> , L.	r-le (2)	(boggy places)	—
<i>Mercurialis perennis</i> , L.	f-le	—	lc
<i>Milium effusum</i> , L.	o	o	—
<i>Molinia coerulea</i> , Moench	r (1)	—	—
<i>Montia fontana</i> , L.	—	l (2)	—
<i>Myosotis arvensis</i> , L.	—	—	rr
„ „ „ var. <i>umbrosa</i> , Bab.	vr (1)	—	—
„ <i>versicolor</i> , Sm.	—	r (1)	—
<i>Nepeta glechoma</i> , Benth.	f-c	f-vc	lc
<i>Nephrodium filix-mas</i> , Rich.	—	—	r
<i>Ophrys apifera</i> , Huds.	—	—	r (2)
„ <i>muscifera</i> , Huds.	r (2)	—	—
<i>Orchis maculata</i> , L.	o	o	—
„ <i>mascula</i> , L.	—	—	r-lf
<i>Oxalis acetosella</i> , L.	f	f-le	—
<i>Pedicularis palustris</i> , L.	—	vr (1, formerly in 2)	—
„ <i>sylvatica</i> , L.	o (2)	—	—
<i>Peplis portula</i> , L.	—	lf-c	o
<i>Picris echioides</i> , L.	—	—	r (1)
<i>Plantago major</i> , L.	—	r-rr	r
<i>Poa annua</i> , L.	—	f-l. ab	o
„ <i>nemoralis</i> , L.	fe-c	—	o
„ <i>pratensis</i> , L.	—	r (1)	o (1)
„ <i>trivialis</i> , L.	f	o	—
<i>Polygonum convolvulus</i> , var. <i>subulatum</i> , L. and C.	—	—	r (1)
<i>Polygonum hydropiper</i> , L.	—	fc-ab	lc
„ <i>lapathifolium</i> , L.	—	r (1)	—
„ <i>mite</i> , Schrank.	—	(1)	—
<i>Potentilla anserina</i> , L.	—	o (2)	—
„ „ „ f. <i>concolor</i>	—	(1)	—
„ <i>erecta</i> , Hampe	o-fe	—	—
„ <i>fragariastrum</i> , Ehrh.	o	—	o-f
„ <i>procumbens</i> , Sibth.	—	r-rr (2)	—
„ <i>reptans</i> , L.	—	r-o	r

TABLE VIII (continued)

Species	Margin of woods and rides	Path	Coppiced Areas
<i>Primula acaulis</i> , L.	—	o
<i>Prunella vulgaris</i> , L. f-r	f-c	r-f
" " <i>forma alba</i>	—	r (1)
<i>Pteris aquilina</i> , L. fc	—	r-l. ab
<i>Ranunculus repens</i> , L. o	o-c	o-vr
" <i>flammula</i> , L.	l (1)	—
<i>Roseda lutea</i> , L.	—	r (1)
<i>Rubus fruticosus</i> (seedlings) c	—	c-ab
<i>Rumex acetosa</i> , L. o	—	o-f
" <i>acetosella</i> , L.	lf (2)	l (1)
" <i>condyloides</i> , Biberst. o-le	o	o-f
" <i>conglomeratus</i> , Murr.	r (1)	—
" <i>obtusifolius</i> , L. r (1)	—	—
<i>Sagina procumbens</i> , L.	lf (2)	o
<i>Sanicula europaea</i> , L.	—	rr
<i>Scabiosa succisa</i> , L. o-fc	r-f	—
<i>Scilla nutans</i> , Sm.	—	r-lc
<i>Scirpus setaceus</i> , L.	lr (2)	—
" <i>sylvaticus</i> , L. r (1)	—	—
<i>Scrophularia aquatica</i> , L. l (1)	—	—
" <i>nodosa</i> , L. o	r	o
<i>Scutellaria galericulata</i> , L.	rr (1)	—
<i>Sedum telephium</i> , L. r (1)	r (1)	—
" " <i>var. purpureum</i> , L. vr (1)	—	—
<i>Senecio aquaticus</i> , Hill l (1, by stream)	—	—
" <i>jacobaea</i> , L. r	r	rr
" <i>sylvaticus</i> , L.	—	o
" <i>vulgaris</i> , L.	—	r
<i>Serratula tinctoria</i> , L. r (1)	—	—
<i>Silene inflata</i> , L.	—	r (1)
<i>Sison, amomum</i> , L. rr	—	—
<i>Sisymbrium alliaria</i> , L. o	—	—
<i>Solidago virg-aurea</i> , L. r-f (3)	—	—
<i>Sonchus asper</i> , Hill r	—	—
" <i>oleraceus</i> , L. r	—	—
<i>Spergula arvensis</i> , L.	—	r
<i>Stachys betonica</i> , Benth. f-fc	r	—
" <i>sylvatica</i> , L.	—	o
<i>Stellaria graminea</i> , L. o (1)	—	—
" <i>holostea</i> , L. o-f	—	o
" <i>media</i> , Vill.	—	r
" <i>uliginosa</i> , Murr.	f (damper parts)	—
" <i>umbrosa</i> , Opiz. vr (1)	—	—
<i>Tamus communis</i> , L. o-f	—	—
<i>Teucrium scorodonia</i> , L. f-vc	—	rr-f
<i>Torilis anthriscus</i> , L. f	—	o
<i>Trifolium minus</i> , Sm.	l (gravelly places)	—
<i>Triodia decumbens</i> , Beauv. o (2)	—	—
<i>Urtica dioica</i> , L. r-f	—	r
<i>Valeriana dioica</i> , L.	l (1)	—
" <i>sambucifolia</i> , Mikan. l (1)	—	—
<i>Verbascum thapsus</i> , L. r	—	rr-lf
<i>Veronica beccabunga</i> , L.	lf (1)	—
" <i>chamaedrys</i> , L. c	f	f
" <i>montana</i> , L.	f	f-fc (damper parts)
" <i>officinalis</i> , L.	lf (drier parts)	f-fc
" <i>serpyllifolia</i> , L.	o-f	r-rr
<i>Vicia angustifolia</i> , L. r (1)	—	—
" <i>sepium</i> , L. f	—	—
<i>Viola hirta</i> , L. l (1)	—	—
" <i>riviniiana</i> , L. f	—	f
" <i>sylvestris</i> , Kit. f	—	f
" " <i>var. punctata</i> , Greg. f	—	f-fc
Totals 227 spp. vars. and formae ...	146	87	117

The marginal society (cf. Table VIII). Owing to the high illumination in many parts of these woods during the Shade-Phase the distinction between the marginal region and the interior is much less marked than in the woods dealt with in Part II. On the other hand the large areas which many of the *Q. sessiliflora* woods occupy furnish sufficiently extended margins in various directions to enable the full effect of aspect to be clearly presented. The commonest members of the marginal flora are *Agrostis alba*, *Asperula odorata*, *Cnicus palustris*, *Digitalis purpurea*, *Epilobium montanum*, *Fragaria vesca*, *Geum urbanum*, *Heracleum sphondylium*, *Holcus mollis*, *Luzula pilosa*, *Melica uniflora*, *Nepeta glechoma*, *Poa nemoralis*, *Potentilla erecta*, *Pteris aquilina*, *Rumex condyglodes*, *Scabiosa succisa*, *Stachys betonica*, and *Teucrium scorodonia*. Of these the most characteristic are the Devil's Bit Scabious, the Betony, Wood Sage, Tormential, and, though less common, *Carex pallescens*, *C. pilulifera*, the Hawkweeds, and Greater Woodrush. Here too are found several rare species whose occurrence though not general is nevertheless significant. Such embrace *Aira flexuosa*, *Carex strigosa*, *Gnaphalium sylvaticum*, *Hypericum androsaemum*, *Lactuca muralis*, *Lathyrus macrorhizus*, *Serratula tinctoria*, *Solidago virgaurea*, and *Triodia decumbens*.

(d) *The Flora of the Coppiced Wood*. As might be expected, the effect of coppicing in these woods is not nearly so pronounced as in the *Q. robur-Carpinus* woods. This is due in part to the more complete tree-canopy, and as a consequence areas in which the trees have been felled appear to offer a closer parallel. A comparison of the data given in Table IX with those for areas occupied by a shrub-layer shows that after coppicing there is an increase of the light-intensity during the Light-Phase of over 27 % and during the Shade-Phase of over 17·7 %. The degree of illumination during the latter, which exceeds 21·5 %, is the more important as so many of the constituents of the flora of coppiced areas are aestival species.

TABLE IX. *Light-intensities in Coppiced Areas*

Wood						Light-Phase %	Shade-Phase %
Sherrard's	80-62	20-10
Brock's	83-62	40 (av.)
Symond's Hyde	70-46·6	16·5 (av.)
Average	67·2	21·6
Approximate increase due to coppicing						+27·5	+17·7

Effects of coppicing. The first and most important effect of coppicing is the great increase of illumination, with consequent increase in the number of species. But in addition there is a marked effect upon the organic content of the surface layer and correlated change in its acidity. Here, as in the *Q. robur-Carpinus* woods, the effect on acidity is in the direction of increase which however would appear to be pronounced for only a short period (cf. Table XI). The observations of Cameron, Baumann and Gully and others have made it appear very probable that the so-called soil acidity is a phenomenon of

adsorption (cf. however E. Truvy, *Journ. Phys. Chem.*, 1916). If this be subsequently established then it must be assumed that the temporary increase of acidity which accompanies the diminution of organic matter is due to an increased adsorptive capacity consequent upon the more rapid decay. It is however easier to explain the results as due to the presence of an actual acid produced during the disintegrating process. The change in humus-content is very pronounced and from the data available (Table X) would seem to depend on a fairly regular diminution of the amount of humus present by approximately 1 % on the dry weight during each period of twelve months. After the first two years the humus-content seems to again increase, owing no doubt to the compensating effect of the developing stools.

TABLE X. *Effect of coppicing on Organic-content*

Wood	Condition	Organic matter %	Decrease %
Sherrard's	Uncoppiced	9.5	} 2
"	Coppiced (2 yrs.)	7.5	
"	Coppiced (3 yrs.)	8.56	} 0.94
"	Uncoppiced	7.34	
"	Coppiced and felled (2 yrs.)	5.8	} 1.54
Brock's	Uncoppiced	7	
"	Coppiced (1 yr.)	6.19	} 0.81
Symond's Hyde	Uncoppiced	6.6	
"	Coppiced (6 months)	6.1	} 0.5
Titnol's	Uncoppiced	6.32	
"	Coppiced (6 months)	5.7	} 0.62
Average uncoppiced		7.35	
Average coppiced		6.25	} 1.10

TABLE XI. *Effect of coppicing on Acidity*

Wood	Condition	Acidity %	Acidity Humus
Sherrard's	Uncoppiced	0.564	1 : 17
"	Coppiced (2 yrs.)	0.464	1 : 16
"	Coppiced (3 yrs.)	0.58	1 : 14.6
Symond's Hyde	Uncoppiced	0.44	1 : 15
"	Coppiced (6 months)	0.51	1 : 12
Cox's	Uncoppiced	0.25	1 : 22
Titnol's	Coppiced (6 months)	0.30	1 : 19

The flora of coppiced areas. The flora of the coppiced areas comprises some 117 species which, as in the case of the *Q. robur-Carpinus* woods (cf. Part II, p. 112), are derived from three sources, namely (a) the original shade-flora; (b) species of the wood-margins and rides; (c) weeds. In the *Q. robur* woods 61.2 % of the species found in the coppiced areas belonged to the second category and the same preponderance is exhibited here. Out of the total of 117 species no less than 89, or 76 %, are found in the uncoppiced condition situated near the edges of the wood or along the paths and rides. Thirty-three species, or 29.2 %, are members of the shade-flora, though many of these are more especially found in the medium shade near the wood-margins. The weeds are only 13 in number and this low percentage (namely 11.1 %), as compared with 29.4 % in the coppiced areas of the *Q. robur* woods, is

mainly attributable to the smaller area of the latter and the consequent proximity of cultivated ground. In these woods one of the most striking features after coppicing is the abundance of Bramble seedlings which grow and persist for several years, but are finally choked out as the stools develop (cf. however, p. 29). The Honeysuckle too develops vigorously where unchecked by the Hornbeam and Brambles. The commonest constituents of the herbaceous vegetation in these areas are *Agrostis alba* (f-c), *Ajuga reptans* (f-c), *Anthoxanthum odoratum* (f-vc), *Arenaria trinervia* (f-c), *Erythraea centaureum* (f-vc), *Fragaria vesca* (f-c), *Galeobdolon luteum* (o-l. ab), *Holcus lanatus* (f-vc), *H. mollis* (f-c), *Hypericum humifusum* (f-c), *Lysimachia nemorum* (c-ab), *Veronica montana* (f-fe), and *V. officinalis* (f-fe). Of these the Centaury, the Soft Grass (*H. mollis*), the Heath St John's Wort and the Yellow Pimpernel are undoubtedly the most characteristic. Particularly noteworthy is the comparative rarity of the Cowwheat (*Melampyrum pratense*) and the Hemp Nettle (*Galeopsis tetrahit*), whilst the Marsh Thistle only attains abundance in the damper parts. The increased number of species in the interior of the woods which results from coppicing and felling is illustrated by the accompanying table. Felled areas as compared with those only coppiced show an appreciably augmented flora. The influence of the time-factor, though not very pronounced, is nevertheless evident.

TABLE XII. *Effect of felling and coppicing upon the number of species*

Wood	Number of species before coppicing	Number of species after coppicing		
		1st yr.	2nd yr.	3rd yr.
Sherrard's	11	25	31	—
Symond's Hyde	12	31	34	—
Sherrard's	(Felled and coppiced)	—	54	69

Compared with the woods on the Clay-with-flints there is a striking absence of those sheets of bloom furnished by such species as *Ficaria verna*, *Anemone nemorosa* and *Conopodium denudatum*. The paucity of the last named and of *Stellaria holostea* is particularly noteworthy. Here as in other oakwoods (cf. Part II, Table XVII, p. 113) certain members of the shade-flora, especially Brambles, Honeysuckle, Yellow Deadnettle, Bugle and Wild Strawberry, exhibit a pronounced increase correlated with the increased illumination, an augmented frequency which disappears with the growing pressure of competition. Those species therefore which normally occupy the shaded areas probably do so because there alone they can compete successfully with those plants which require greater illumination.

(e) *Colonisation*. Generally artificial restriction gives to the woodland periphery a sharply defined limit so that colonisation and consequent extension of the afforested area is seldom met with. Here and there however, where adjacent "rough" land has been allowed to develop naturally, scrub appears of which saplings of *Betula* are a prominent and often abundant constituent.

Such scrub is seen in an intermediate condition at Bricket Wood Scrubs, in an advanced stage at Hertford Heath, and in an early phase on the south-west border of Wormley Wood. As the two former have already been described by the present writer (*Ecology of Scrub, loc. cit.*) they need not be considered in detail here. It is however important to recognise the fact that the herbaceous flora in these areas of scrub is remarkably similar to that of the wood margin of the *Q. sessiliflora*-*Carpinus* woods, and the same is true with regard to the scrub on Clay-with-flints and the marginal flora of the *Quercus robur* woods. All the three areas quoted above are very wet even in summer and this may perhaps account for the rarity of young trees of *Q. sessiliflora*, for we have noted how in woods of this species the Common Oak tends to become prevalent in the damper hollows. The same edaphic feature is probably responsible for the large proportion of Hazel accompanying the Hornbeam. But even having regard to these departures from the normal it may be said that the scrub-covered areas do tend to emphasise the natural character of the plant aggregates which we have here recognised.

The wet character of the rides in these woods which has often been emphasised above makes it scarcely surprising that *Fraxinus excelsior* is often a conspicuous coloniser where these are allowed to become overgrown.

Areas which have been coppiced sometimes exhibit numerous seedlings of *Populus tremula* and these give rise to the local thickets of this tree found in the uncultivated wood.

Seedlings of either species of Oak are comparatively scarce, and this is largely a result of the prevalence of rabbits on these light soils. In Wormley Wood where the soil is heavier and too damp to be suitable for these rodents, Oak saplings are frequent. But usually seedlings of the Common Oak are more prevalent than those of the Durmast Oak which is probably to be attributed to the freer fruiting of the former.

(5) The Cryptogamic Flora

(a) *Musci*. Most of the Mosses common in these woods are also frequent in those dominated by the Common Oak, though *Polytrichum formosum*, *Dicranum scoparium*, and *Fissidens bryoides* are generally more abundant. Of those species that appear to be especially characteristic may be mentioned *Dicranella heteromella*, *Leucobryum glaucum*, *Mnium punctatum*, *Polytrichum juniperinum*, and in one wood *Tetraphis pellucida*¹ and *Plagiothecium undulatum*. The Moss-flora is as a whole richer both in species and individuals than in the woods of Common Oak. The abundance of *Dicranella heteromella* is a noteworthy feature of the sides of the woodland streamlets. In such situations it grows in great abundance together with the Liverwort *Calypogeia fissus*² and forms a definite cryptogamic society. The damper and more shaded

¹ Kessler (*Beih. z. Bot. Centralbl.* 31, pp. 358-387, 1914) has shown that the spores of *Tetraphis pellucida* will only germinate in an acid medium.

² This species is characteristic of the *Q. sessiliflora* woods of Somerset.

parts of these woods are frequently occupied by a Moss-society composed of most of the commoner species (cf. Table XIII). This may be regarded as the parallel, under conditions of lower rainfall, to the cryptogamic ground-flora of the *Q. sessiliflora*-woods in the coombs and gills of Somerset and

TABLE XIII. *List of Musci*

<i>Amblystegium serpens</i> , Bruch and Schimper	...	r (1)
<i>Anomodon viticulosus</i> , Hook. and Tayl.	...	o (1)
<i>Aulacomnium androgynum</i>	...	o
<i>Barbula fallax</i> , Hedw.	...	vr (1)
<i>Brachythecium albicans</i> , B. and S.	...	(1)
" <i>purum</i> , Dixon	...	fe-c
" <i>rutabulum</i> , B. and S.	...	f
<i>Bryum pendulum</i> , Schimp.	...	o (1)
<i>Camptothecium sericeum</i> , Kindb.	...	r (1)
† <i>Catharina undulata</i> , W. and M.	...	c-vc
<i>Dicranella heteromella</i> , Schimp.	...	c-ab
" <i>rufescens</i> , Schimp.	...	f-c
§ <i>Dicranum scoparium</i> , Hedw.	...	f-fe
<i>Eurhynchium confertum</i> , Milde	...	(1)
" <i>myurum</i> , Dixon	...	o
" <i>piliferum</i> , B. and S.	...	o-f
" <i>praelongum</i> , Hobkirk	...	le-c
" <i>rusciforme</i> , Milde	...	f
" <i>striatum</i> , B. and S.	...	f-le
" <i>swartzii</i> , Hobkirk	...	l
<i>Fissidens bryoides</i> , Hedw.	...	o-le
" <i>taxifolius</i> , Hedw.	...	r-le
<i>Homalia trichomanoides</i> , B. and S.	...	lf-r
<i>Hylocomium splendens</i> , B. and S.	...	f
<i>Hypnum cordifolium</i> , Hedw.	...	l (1)
† " <i>cuspidatum</i> , L.	...	l
" <i>eupressiforme</i> , L.	...	c
" " <i>var. resupinatum</i> , Schimp.	...	r
† " <i>schreberi</i> , Willd.	...	f
" <i>squarrosus</i> , L.	...	f-c (path)
" <i>triquetrum</i> , L.	...	l-f
† <i>Leucobryum glaucum</i> , Schimp.	...	lf (Pteris society)
<i>Mnium affine</i> , Bland	...	l, vc (1)
† " <i>hornum</i> , L.	...	c
" <i>punctatum</i> , L.	...	l-lf
" <i>undulatum</i> , L.	...	rr
<i>Orthotrichum affine</i> , Schrad.	...	rr
§ <i>Plagiothecium denticulatum</i> , B. and S.	...	rr-c
" <i>elegans</i> , Schull	...	f
" <i>sylvaticum</i> , B. and S.	...	o
† " <i>undulatum</i> , B. and S.	...	rr (1)
<i>Pleuridium subulatum</i> , Rabenh.	...	l (1)
† <i>Polytrichum aloides</i> , Hedw.	...	l (1)
§ " <i>formosum</i> , Hedw.	...	c
" <i>juniperinum</i> , Willd.	...	lc
" <i>nanum</i> , Neck.	...	rr (1)
<i>Porotrichum alopecurum</i> , Mitt.	...	lf-l, ab (1) (Ficaria-Adoxa society)
<i>Sphagnum cymbifolium</i> , Ehrh.	...	l (2)
†§ <i>Tetraphis pellucida</i> , Hedw.	...	rr (1)
<i>Thuidium tamariscinum</i> , B. and S.	...	f-c

The species marked with a dagger (†) are stated by Watson (*New Phytologist*, vol. VIII, p. 92) to be characteristic of the Oakwoods of Somerset (? *Q. sessiliflora*). Those marked § are characteristic of the *Q. sessiliflora* woods of Derbyshire (cf. Moss, *l.c.*).

Yorkshire, which is likewise developed where the light-intensity is low and the water-content high. *Eurhynchium praelongum* is particularly frequent where the chalk is close to the surface and there too the unattached form of *Porotrichum alopecurum* is sometimes abundant.

(b) *Hepaticae*. The often abundant Liverwort-flora is a marked contrast to the meagre occurrence of these plants on the Clay-with-flints. This increase is probably to be attributed to the more open texture of the soil and the proximity of the permanent water-table. The most frequent species are: *Alicularia scalaris*, *Aplozia crenulata*, *Calypogeia fissa*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *Lophocolea bidentata*, *L. heterophylla*, *Pellia fabbroniana*, *Plagiochila asplenoides* var. *humilis*, and *Scapania nemorosa*. The last two species are usually most frequent in the *Dicranella-Calypogeia* society mentioned above. In no case has *Metzgeria furcata* or *Radula complanata* been encountered in a wood of this type, although the former is quite common on the tree-trunks of the *Q. robur* woods and the latter is not infrequent. *Madotheca platyphylla* which occurs in the *Q. robur* woods is here confined to the tree trunks where the soil has a low acidity. 33 species of *Hepaticae* have been recorded (cf. Table XIV) in all. This is a small number as compared with the Hepatic flora in the *Q. sessiliflora* woods of the West, but considerably in excess of that in the Derbyshire woods (viz. 21 spp., cf. Moss, *loc. cit.*).

TABLE XIV. *List of Liverworts*

<i>Alicularia scalaris</i> , Corda	lf-c
* <i>Aneura multifida</i> L.	(1)
<i>Aplozia crenulata</i> , Dum.	f-c
" " " var. <i>gracillima</i> , Sm.	f
" <i>sphaerocarpa</i> , Dum.	r (1)
<i>Calypogeia fissa</i> , Raddi	vc-lf
" <i>trichomanis</i> , Corda	r (2)
<i>Cephalozia bicuspidata</i> , Dum.	c-f
* " <i>byssacea</i> , Warnst.	(2)
<i>Chiloscyphus pallescens</i> , Dum.	r (1)
" <i>polyanthus</i> , Corda	f-absent
<i>Conocephalum conicum</i> , Dum.	c (1)
<i>Diplophyllum albicans</i> , Dum.	vc-f
<i>Eucalyx hyalinus</i> , Breidel	r-f (3)
<i>Fossombronina pusilla</i> , Dum.	rr-f
<i>Frullania dilatata</i> , Dum.	vr (3)
" <i>tamarisci</i> , Dum.	vr (2)
* <i>Lejeunia cavifolia</i> , Lindb.	(2)
<i>Lepidozia reptans</i> , Dum.	rr (2)
<i>Lophocolea alata</i> , Mitt.	o-r (2)
" <i>bidentata</i> , Dum.	c-f
" <i>heterophylla</i> , Dum.	f-c
* <i>Lophozia incisa</i> , Dum.	(1)
<i>Madotheca platyphylla</i> , Dum.	r (1)
<i>Pellia epiphylla</i> , Corda	r
" <i>fabbroniana</i> , Raddi	lc-f
<i>Plagiochila asplenoides</i> , var. <i>humilis</i> , Lindb.	lf-c
<i>Riccia crystallina</i> , L.	r (1)
" <i>sorocarpa</i> , Bisch.	lr (1)
* <i>Ricciocarpus natans</i> , Corda	r (1)
<i>Scapania curta</i> , Dum.	vr (1)
" <i>dentata</i> , Dum.	l (1)
" <i>irrigua</i> , Dum.	f (1)
" <i>nemorosa</i> , Dum.	c-rr
" <i>undulata</i> , Dum.	r (2)
* <i>Trichocolea tomentella</i> , Dum.	r (1)

* These six species were recorded from one or two woods of this type by the late Mr A. E. Gibbs ("List of Hertfordshire Hepatics," *Trans. Herts. Nat. Hist. Soc.*, vol. vii, pp. 233-236, 1893) but have not been observed by the writer. It is therefore probable that they are all of rare or very local occurrence. See also Salisbury, "New records of Hertfordshire Hepatics," *Trans. Herts. Nat. Hist. Soc.*, vol. xvi, pt 4, 1917.

(c) *Algae*. In the *Q. robur-Carpinus* woods the only common terri-colous Alga is *Hormidium flaccidum*, A. Br., which species also occurs in the *Q. sessiliflora* woods. The commonest and most characteristic Alga of the latter however upon the paths and rides is *Zygnema ericetorum*, Hansg. (cf. Fritsch, "Morphology and Ecology of *Zygnema ericetorum*," *Annals of Botany*, vol. xxx, pp. 135-149, 1916), often associated with the liverwort *Alicularia scalaris*. *Mesotaenium violascens*, De Bary, and the *Dactylococcus*-stage of *Scenedesmus obliquus*, Kuetz., are sparsely met with, particularly amongst the leaves of *Bryum*, upon the ground, or amongst Mosses such as *Homalia* and *Hypnum*, upon the tree-trunks. Here too *Gloeocystis vesiculosa*, Naeg., is sometimes encountered. The algal flora may therefore be said to resemble that of heaths (cf. Fritsch and Salisbury, "Further Observations on the Heath Association on Hindhead Common," *New Phytol.*, vol. xiv, p. 134, 1915). One rare Alga, namely *Microcoleus vaginatus*, Gom., is locally frequent upon the paths in a wood of this type situated upon the Boulder Clay.

In view of the high acidity of the soil of these woods it is significant that the algal flora is strikingly similar to that described by Petersen as characteristic of soils with an acid reaction ("Stud. over Danske Acrofile Alger," *Mem. de l'Acad. Roy. d. Sc. et d. Lettr. de Danemark*, t. xii, p. 360, 1915). Moreover, the greater abundance of *Hormidium flaccidum* in the *Q. robur* woods is also in conformity with the characteristic frequency of species of this genus on neutral or alkaline soils. Very few Diatoms have been observed, a sparsity which Petersen noted in the woods and forests of Denmark and which may be an outcome of the prevailing high acidity.

(d) *Lichens*. The members of this group have only been extensively collected in Sherrard's Park and Symond's Hyde Woods. The frequencies apply to the former of these areas only, but with regard to the commoner species a wider application can in most cases be assumed. For the identifications I am entirely indebted to Mr R. Paulson, F.L.S. It may be safely asserted that the Lichen-flora of these woods is much richer than that of the *Q. robur-Carpinus* woods, for not only are there fewer species in the latter, but such as occur are more sparingly distributed.

TABLE XV. *List of Lichens.*

Calcium hyperellum, Ach.	o
Cladonia digitata, var. denticulata, Hoffm.	vr
„ furcata, Hoffm.	lf
„ macilenta, Hoffm.	ab
„ pyxidata, Fr.	lf
„ squamosa, Hoffm.	o
Evernia prunastri, Ach.	c
Graphis elegans, Ach.	c
Lecanora albella, Ach.	vc
„ chlarona, Nyl.	o
„ parella, var. turneri, Nyl.	o
„ rugosa, Nyl.	r
„ varia, Ach.	ab

TABLE XV (*continued*)

<i>Lecidea griffithsii</i> , Masul	r
„ <i>quernea</i> , Ach.	
„ <i>uliginosa</i> , Ach.	
<i>Opegrapha herpetica</i> , Ach.	r
<i>Parmelia borreri</i> , Turn.	rr
„ <i>caperata</i> , Ach.	c
„ <i>fuliginosa</i> , var. <i>laetevirens</i> , Nyl.	c
„ <i>physodes</i> , var. <i>labrosa</i> , Ach.	ve
„ <i>saxatilis</i> , Ach.	c
„ <i>sulcata</i> , Tayl.	f
<i>Peltigera spuria</i> , Leight.	lf
„ <i>polydactyla</i>	lf
<i>Pertusaria amara</i> , Nyl.	c
„ <i>communis</i> , DC.	f
„ <i>globulifera</i> , Nyl.	o
„ <i>wulfenii</i> , DC.	rr
<i>Platysma glaucum</i> , Nyl.	o
<i>Thelotrema lepadinum</i> , Ach.	f
<i>Usnea florida</i> , Ach.	c
„ <i>hirta</i> , Hoffm.	f
<i>Verrucaria viridula</i>	r

(The species referred to in Part I under the name of *Parmelia perlata* as occurring commonly in the *Q. robur* woods is probably *P. sulcata*.)

(e) *Fungi*. It is hoped to give subsequently in conjunction with Mr Ramsbottom a complete account of the Fungus-flora of these woods. The list of species will not therefore be given here. It should however be stated that, inclusive of those previously recorded (*vide Trans. Herts. Nat. Hist. Soc. excursion lists*), over 450 species have been observed in woods of this type. The character of the Fungus-flora is distinctive and far richer than that of the *Q. robur-Carpinus* woods. As indicative of its general facies it may be mentioned that the following species are a few of those generally distributed and appear to be more or less confined to the *Q. sessiliflora-Carpinus* woods, viz. *Boletus parasiticus*, *Craterellus cornucopoides*, *Nyctalis asterophora*, *N. parasitica*, *Scleroderma vulgare*, *Stropharia aeruginosus*, and *Thelephora laciniata*.

(f) *Mycetozoa*. The members of this group have not been studied, and the list of species in Table XVI recorded from the woods dealt with in this paper is extracted from the local lists and two communications by Mr J. Saunders in the *Transactions of the Hertfordshire Natural History Society*, vol. VII, pp. 144, 145, 1893 and vol. VIII, p. 71, 1895.

TABLE XVI. *List of Mycetozoa*

<i>Arcyria cinerea</i>	<i>Stemonitis ferruginea</i>
„ <i>incarnata</i>	<i>Trichia affinis</i>
<i>Fuligo septica</i>	„ <i>fragilis</i>
<i>Hemiarcyria clavata</i>	„ <i>jackii</i>
<i>Leocarpus fragilis</i>	„ <i>scabra</i>
<i>Lycogala epidendrum</i>	„ <i>varia</i>
<i>Physarum leucophaeum</i> .	

(6) **Fauna**

Rabbits are the only common mammals in these woods and they play an important rôle in determining the succession phases (see p. 29). The immunity of Bracken and Brambles from their ravages has been remarked and the same feature with regard to the former species was observed in the Breckland by Farrow (*Journal of Ecology*, vol. v, p. 6). Squirrels are not infrequent and often damage the shoots of young trees. There is no indication that any of the other larger animals directly affect the vegetation, though in a state of nature there can be little doubt that multiplication of the already frequent stoats would greatly diminish the effects of the rabbits.

Amongst the Lepidoptera *Tortrix viridiana* is often exceptionally abundant, and its larvae, which mainly attack the leaves of the Hornbeam, often reduce the assimilatory area of the latter by from 30-50 %.

Perhaps the most interesting aspect of the lower fauna is the poverty both of species and individuals, thus affording a parallel to the sparse flora. This feature is probably to be correlated with the prevalent high acidity. In this connection my friend Dr A. E. Boycott, F.R.S., has kindly made a comparison for me of the Molluscan fauna in two parts of Sherrard's Wood, viz. (1) in the *Q. sessiliflora-Carpinus* wood, and (2) from beneath Beech trees on the edge of the Oak Wood situated at the foot of the Reading Bed escarpment on the chalk outcrop. From the former habitat two species only were noted, viz., *Helix rotundata* and *Arion hortensis*, whilst from the latter no less than 18 species were observed. The number of Beetles, Spiders, etc., also showed a similar relation.

PART IV. COMPARATIVE RESULTS

(1) **Comparison of the *Q. robur-Carpinus* and *Q. sessiliflora-Carpinus* woods**

(a) *Edaphic conditions.* A study of the data given in Tables IV, XI, Part II and Tables II and III, Part III, shows that the humus-content is lower (average for *Q. s.* = 8.5 %, for *Q. r.* = 10.4 %) and the proportion of silt and clay is smaller in the soil of the *Q. sessiliflora-Carpinus* woods than in that of the *Q. robur-Carpinus* woods. This naturally involves a diminished water-content, and estimations based on soil-samples taken from the two types on the same day (Table XVII) bear out such an assumption. Hence the ground-flora is essentially that of drier types of soil in spite of the close proximity of the water-table.

Moreover if we compare the average of all the estimations of water-content the woods of Common Oak show 33 % on the dry weight as compared with 29.5 % for the Durmast Oak woods.

TABLE XVII. *Water-contents of composite soil-samples, all collected on the same day after heavy rainfall (13/11/15)*

Locality	Type	Water-content %
Symond's Hyde ...	Q. sess.-Carp.	34.1
" " " " " "	" "	36.2
Titnol's " " " "	" "	24.5
" " " " " "	" "	26.9
Cox's " " " "	Q. sess.-Q. r.-Carp.	32.0
" " " " " "	" "	33.2
Langley " " " "	Q. robur-Carp.	40.12
" " " " " "	" "	40.30
Cutt's Green " " " "	" "	40.20
" " " " " "	" "	40.30
Puddler's " " " "	" "	34.7
" " " " " "	" "	35.4

Av. 31.1

Av. 38.5

The absolute acidity of the two types irrespective of water-content shows 0.41 % for the *Q. sessiliflora* and 0.44 % for the *Q. robur* woods. But we have noted that the acidity-humus ratios indicate a higher acidity for the former, and if we divide the acidity by the average water-content in each case the result shows a very slightly higher acidity for the *Q. sessiliflora* woods. In this connection it is important to recognise the influence of the permanent water-table. It is well known that the present plane of permanent saturation in Hertfordshire is much lower than in times past, a fact sufficiently borne out by the obsolete and obsolescent streams. This implies that formerly the surface soil in the *Q. sessiliflora* woods was water-logged and consequently though the soil-solution would be more dilute this was doubtless more than compensated for by the absence of aeration. In these woods as on several of our commons (cf. Salisbury, *Trans. Herts. Nat. Hist. Soc.* vol. xv, p. 71, 1915) the decrease in amount of *Calluna* and the growing rarity of other peat-lovers is pronounced. At the time then when the present distribution of the two species of Oak was determined one may well suppose that the differences in acidity were more pronounced than now. The electrical resistances (cf. Table XVIII) of solutions obtained with distilled water from air-dried samples (cf. p. 23) indicate that the soluble mineral salts present are more abundant in the soils from *Q. robur* woods. In view of the very considerable dilution the difference in ionisation is most likely negligible. Hence we can probably regard the resistances so obtained as approximately inversely proportional to the percentage of electrolytes present. On this assumption the soluble salts in the soil of the *Q. robur* woods probably amount to over 50 % more than in that of the *Q. sessiliflora* woods.

(b) *Floristic differences. The trees and shrub-layers.* The following are present in the *Q. sessiliflora*-*Carpinus* woods, but absent from the *Q. robur*-*Carpinus* woods: *Populus alba*, *Pyrus communis*, *Rhamnus catharticus*, *R. frangula*, *Ribes rubrum*, *Rosa stylosa*, *R. tomentella*, and *R. tomentosa*. All of these are either very rare or rare, though *Rhamnus frangula* may be regarded as a characteristic species.

TABLE XVIII. *Electrical resistances of soil-solutions*

Locality	Type	Ground-flora	Resistance in ohms
Titnol's ...	Q. sess.-Carp.	Mercurialis dom.	1100
Symond's Hyde ...	"	Pteris dom.	1100
Brook's ...	" (coppiced)		1150-1550
Cow Heath ...	"	Pteris dom.	1200
Sherrard's ...	"	Nepeta dom.	1400
" ...	"	Scilla dom.	1450
" ...	"	Mercurialis dom.	1100
" ...	"	Ficaria-Adoxa dom.	700
Pinner (Middlesex) ...	"	Pteris dom.	1400
" ...	"	Dense shrub-layer	1550
Ball's ...	Q. robur-Carp.	Sparse	1500
Sauney ...	"	Anemone dom.	650-400
Ambrose ...	"	Scilla-Mercurialis	700
Cutt's Green ...	"	Anemone dom.	650
Average ...		{ Q. sess.-Carp. 1245 Q. robur-Carp. 780	

Of much more interest is the fact that several trees and shrubs found in the Oak woods of Hertfordshire are only met with in those of the Common Oak where the Durmast Oak is also present. Such are *Pyrus aucuparia*, *P. torminalis*, *Prunus insititia*, and *Viburnum opulus*, all, except the Bullace, species that occur characteristically in *Q. sessiliflora* woods elsewhere. The Holly, the Red Birch, and the Ling are all much more frequent than in the *Q. robur* woods. On the other hand *Prunus avium* is much less common and the Lime is usually absent. *Clematis vitalba*, which is local on the Clay-with-flints, in these woods is confined to the chalk-pits. The most striking feature is however undoubtedly the abundance of Brambles and Honeysuckle¹ which only attain any considerable frequency in those *Q. robur* woods where *Q. sessiliflora* is also present.

The ground-flora. In the herbaceous flora the distinctions are much more numerous. Some 56 species are met with in the woods of Durmast Oak, which are not present in the Common Oak woods, but the absence of some of these is doubtless purely accidental. Those probably to be regarded as characteristic and which are of frequent or common occurrence are: *Carex pallescens* (o-le), *C. pendula* (lf-f), *Eupatorium cannabinum* (lf, 2), *Juncus bufonius* (lf-fc), *Lotus major* (o-f), *Luzula maxima* (f-rr), and *Polygonum hydropiper* (fc-ab). Other characteristic but uncommon species also absent from the *Q. robur*-*Carpinus* woods are *Aira flexuosa*, *Carex pilulifera*, *C. pseudo-cyperus*, *C. strigosa*, *Chrysosplenium oppositifolium*, *Menyanthes trifoliata*, *Molinia coerulea*, *Montia fontana*, *Nephrodium montanum*, *N. spinulosum*, *Pedicularis palustris*, *Potentilla procumbens*, *Scirpus setaceus*, *S. sylvaticus*, *Serratula tinctoria* and *Triodia decumbens*. Other species characteristic of the *Q. sessiliflora* woods though absent from the typical *Q. robur* woods are met with in those where *Q. sessiliflora* is also present. They include *Angelica sylvestris*, *Blechnum spicant*, *Callitriche stagnalis*, *Hypericum androsaemum*, *H. tetra-*

¹ This same feature is exhibited in the *Q. sessiliflora*-*Carpinus* woods at Pinner.

pterum, *Lathyrus macrorhizus*, *Luzula multiflora*, *Pedicularis sylvatica*, *Potentilla erecta*, *Scabiosa succisa*, *Scutellaria gulericulata*, *Stellaria uliginosa*, and *Nephrodium dilatatum*. Several species show considerable differences in their frequency in the two types of wood (cf. Table XIX).

TABLE XIX. *Comparative Frequencies*(1) *More abundant in Q. robur-Carpinus woods:*

Species	Q. sess.-Carp.	Q. robur-Carp
* <i>Anemone nemorosa</i> ...	rr-lc	vc-ab
<i>Arenaria trinervia</i> (copp.) ...	f-c	c-vc
<i>Arum maculatum</i> ...	lf	f-c
<i>Barbarea vulgaris</i> (copp.) ...	rr	la
<i>Cnicus palustris</i> (copp.) ...	f-l. ab	c-vc
<i>Conopodium denudatum</i> ...	rr-f	f-vc
* <i>Dipsacus sylvestris</i> ...	o	rr-lc
<i>Ficaria verna</i> ...	r-l. ab	c-ab
<i>Galeopsis tetrahit</i> (copp.) ...	r	c-vc
<i>Geranium dissectum</i> ...	rr	f-c
<i>Hypochaeris radicata</i> ...	r-o	r-lc
* <i>Mercurialis perennis</i> ...	l. ab-rr	ab-vc
<i>Primula acaulis</i> ...	r-f	f-rr
<i>Ranunculus auricomus</i> ...	lr	fc-r
* <i>Sanicula europaea</i> ...	rr-f	f-vc
* <i>Scilla nutans</i> ...	rr-l. ab	ab
<i>Scrophularia nodosa</i> ...	o	o-f
<i>Sisymbrium alliaria</i> (edge) ...	o r	f-c
<i>Stellaria holostea</i> (edge) ...	o-f	f-vc

Species marked * were found by Wilson (*loc. cit.*) to be either occasional or absent in the *Q. sessiliflora* woods of Surrey on the London Clay, but common in the *Q. robur* woods on the Clay-with-flints.

(2) *More abundant in the Q. sessiliflora-Carpinus woods:*

<i>Cardamine flexuosa</i> ...	f (London Clay)	r (1)
<i>Epilobium montanum</i> ...	f-c	o-f
<i>Erythraea centaureum</i> (copp.) ...	i-vc	f-c (light soils)
<i>Fragaria vesca</i> ...	c-f	f-r
<i>Galium palustre</i> ...	fc	o (1)
<i>Holcus mollis</i> (copp.) ...	f-c	r-vc (light soil)
<i>Hypericum humifusum</i> (copp.) ...	f-c	r
† „ <i>pulchrum</i> (copp.) ...	o-r	vr
„ <i>tetrapterum</i> ...	o-f	r
† <i>Luzula pilosa</i> ...	o-fc	o-f
<i>Lysimachia nemorum</i> (path and copp.) ...	c-ab	r-f
<i>Peplis portula</i> (path) ...	lf-c	o (1)
† <i>Pteris aquilina</i> ...	l. ab-o	r (ab. in 2)
† <i>Stachys betonica</i> (edge) ...	f	r
† <i>Teucrium scorodonia</i> ...	f-c	f
<i>Veronica officinalis</i> (path and copp.) ...	f-fc	r

Species marked † were found by Wilson to be occasional or absent in the *Q. robur* woods on clay-with-flints and common in the *Q. sessiliflora* woods on the London Clay.

About 50 species are present in the *Q. robur* woods which are absent or very rare in the *Q. sessiliflora* woods, but most of these are not of sufficient importance to particularise. The more characteristic are *Galeopsis ladanum*, *Geranium molle*, *Helleborus viridis*, *Iris foetidissima*, *Lychnis dioica*, *Melilotus officinalis*, *Pimpinella major*, *Plantago lanceolata*, *Polygonum aviculare*, *P. persicaria*, and *Solanum nigrum*.

The differences in the vegetation of the coppiced areas are equally striking, for whilst in the *Q. robur* woods *Cnicus palustris* and *Galeopsis tetrahit* are abundant, in the *Q. sessiliflora* woods these species occur but rarely. Other characteristic species of the former which are infrequent or rare in the coppiced areas of the latter are *Geranium dissectum*, *Barbarea vulgaris*, *Stellaria holostea*, *S. graminea*, *Dipsacus sylvestris*, and *Verbascum thapsus*. *Holcus lanatus* too is usually replaced in *Q. sessiliflora* woods by *Holcus mollis*. On the other hand *Hypericum humifusum*, *Lysimachia nemorum*, *Erythraea centaureum*, and *Veronica officinalis* are common here and infrequent in the *Q. robur* woods.

The foregoing floristic differences emphasise the calcicolous facies of the herbaceous flora in the *Q. robur* woods and its calcifugous character in the *Q. sessiliflora* woods. From this point of view it is interesting to note that R. W. Scully (*Flora of County Kerry*, pp. xliv–xlvi, Dublin, 1916) enumerates the following in his list of calcicole species: *Barbarea vulgaris*, *Sisymbrium alliaria*, *Arenaria trinervia*, *Pimpinella major* and *Verbascum thapsus*, all of which are much more frequent in the *Q. robur* woods. Again the following which are characteristic of the *Q. sessiliflora* woods are stated to be calcifuge: *Stellaria uliginosa*, *Montia fontana*, *Hypericum humifusum*, *H. pulchrum*, *Lathyrus macrorhizus*, *Potentilla erecta*, *Chrysosplenium oppositifolium*, *Peplis portula*, *Galium saxatile*, *Gnaphalium uliginosum*, *Calluna vulgaris*, *Menyanthes trifoliata*, *Digitalis purpurea*, *Pedicularis* spp., *Polygonum hydropiper*, *Luzula maxima*, *L. multiflora*, *Carex binervis*, *Molinia coerulea*, *Pteris aquilina*, *Blechnum spicant*, and *Nephrodium montanum*. The calcifuge tendency of both *Q. sessiliflora* and *Carpinus betulus* has already been dealt with, so that we see this aspect emphasised in trees, shrubs, and herbs alike. Indeed the *Q. robur*-*Corylus* woods, the *Q. robur*-*Carpinus* woods, and the *Q. sessiliflora*-*Carpinus* woods form a series in which the flora becomes more and more calcifuge in character. By the term calcifuge as used here it must however be understood that a distribution normally confined to siliceous soils is implied. It is probably pressure of competition rather than preference that is mainly responsible for the restriction of calcifuge species to siliceous soils.

(2) Comparison with other *Q. sessiliflora* woods

The most detailed account of the vegetation of *Q. sessiliflora* woods in this country is that given by Moss (*loc. cit.*) for those of Derbyshire. Comparison with the Hertfordshire woods shows that of the 231 native species enumerated by that author 73 are not represented in the *Q. sessiliflora* woods of Hertfordshire, whilst the flora of the latter includes 109 species which do not occur in the Derbyshire woods. Of the 153 species, exclusive of varieties, common to both, the most pronounced feature is the close correspondence exhibited by the frequencies in these two such widely separated counties: a fact which not only emphasises the natural character of the ecological

assemblage but also serves to indicate the importance of edaphic and biological as compared with minor climatic differences. The most important discrepancies between the frequencies of species found in the two regions are given in the following table.

TABLE XX: *Frequencies in Q. sessiliflora woods of Hertfordshire and Derbyshire*

Species	Hertfordshire	Peak District
<i>Agrostis vulgaris</i>	r	l. ab
<i>Aira flexuosa</i>	r	l. sd
<i>Ajuga reptans</i>	f-le	l-o
<i>Anemone nemorosa</i>	rr-lf	l. ab
<i>Asperula odorata</i>	rr-f	l. ab
<i>Cardamine flexuosa</i>	f	o
<i>Carex pallescens</i>	o-le	vr
<i>Chrysosplenium oppositifolium</i>	lf (2)	l. ab
<i>Epilobium montanum</i>	f-c	o
<i>Galeobdolon luteum</i>	f-c	o
<i>Galium aparine</i>	f	l. ab
<i>Hypericum perforatum</i>	f	r
<i>Luzula maxima</i>	rr-f	l. ab
<i>Lysimachia nemorum</i>	c	r-o
<i>Mercurialis perennis</i>	rr-l. ab	o
<i>Molinia coerulea</i>	r (1)	l. ab
<i>Nepeta glechoma</i>	fc	r-o
<i>Poa nemoralis</i>	fc-c	vr
<i>Athyrium filix-foemina</i>	vr	o-la
<i>Nephrodium montanum</i>	vr	l. ab

Of the species absent from the Derbyshire woods but present in those of Hertfordshire the great majority are of rare or uncommon occurrence, but those of greater frequency include *Agrostis alba*, *Brachypodium sylvaticum*, *Callitriche stagnalis*, *Erythraea centaureum*, *Eupatorium cannabinum*, *Euphorbia amygdaloides*, *Galium palustre*, *Gnaphalium uliginosum*, *Hypericum humifusum*, *H. tetrapterum*, *Luzula multiflora*, *Peplis portula*, *Poa annua*, *Polygonum hydropiper*, *Ranunculus repens*, *Scabiosa succisa*, *Stellaria uliginosa*, and *Veronica officinalis*. It will be noted that the most common of these are species characteristic of the paths and rides.

The more important species of the Peak district woods absent from those of Hertfordshire are *Carex laevigata*, *Equisetum sylvaticum*¹, *Geum rivale*, *Lychnis dioica*, *Myrrhis odorata*, *Petasites ovatus*, *Prunus padus*, and *Vaccinium myrtillus*. The remainder are either rare or only of local occurrence.

Finally we may note that many of the species common in the disused quarries, passing into *Q. sessiliflora* wood, described by Mr Margerison (Bradford, 1909), are those characteristic of the woods here dealt with (compare also Rübel, *New Phytol.* vol. xi, p. 55, 1912).

¹ In general species commonly associated with peaty soil are more frequent in the *Q. sessiliflora* woods of Derbyshire, Wales and Somerset, than in those of Hertfordshire. Indeed as might perhaps be expected the *Q. sessiliflora*-*Carpinus* woods exhibit a vegetation that has something in common with that of the lighter types of clays and so as it were connect the Durmast Oak woods of acid siliceous soils on the one hand with the *Q. robur*-*Corylus* woods of nearly neutral clays on the other.

THE AQUATIC AND MARSH VEGETATION OF ESTHWAITE WATER

By W. H. PEARSALL

(With twelve figures in the Text)

Continued from Vol. 5, p. 202

V. THE MARSH AND FEN VEGETATION OF ESTHWAITE WATER

The terrestrial hydrophytic vegetation at Esthwaite falls naturally into two subdivisions:

A. The purely *zonal* plant communities bearing no relation to the aquatic succession.

B. The communities succeeding aquatic plants as the mud gets above the water level.

I propose to refer to these two types of communities respectively as *marsh* and *fen* types, since the habitats, plant communities, and biotic relationships of each are widely different.

A. The **marsh vegetation** occurs in zones near the water, and is confined to substrata composed of the primitive rounded morainic stones of which the shores are built. Locally, these are superficially eroded, or masked by thin peat, but these variations produce little difference in the vegetation, which is apparently chiefly controlled by the stony substratum and the slightly acid waters of the lake. The following communities are distinguished.

(i) Along sheltered, slightly eroded and unsilted parts of the shore, local communities of *Eleocharis palustris* or *Phalaris arundinacea* occur, extending sometimes below the summer level, and to about 10–15 cm. above it, with *Lythrum Salicaria* frequent. All three species have tough rhizomes capable of penetrating the interstices of the hard substratum. Where peat accumulates or silting sets in, these communities pass into the *Phragmites* consociates. The communities being developmental and having one dominant each, can be termed respectively the *Eleocharis palustris* consociates and *Phalaris arundinacea* consociates.

(ii) Where pasture land abuts on the lake, an open community of the following species occurs, usually at levels of 10–30 cm. above the summer water level.

* <i>Ranunculus Flammula</i>	f	<i>Lythrum Salicaria</i>	o
<i>Caltha palustris</i>	l	<i>Hydrocotyle vulgaris</i>	f
<i>Potentilla palustris</i>	l	<i>Achillea Ptarmica</i>	f

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<i>Senecio aquaticus</i>	l	* <i>J. conglomeratus</i>	l
<i>Hypochaeris radicata</i>	o	* <i>J. articulatus</i>	ab
<i>Lysimachia Nummularia</i>	l. ab	<i>Carex Goodenowii</i>	o
<i>Myosotis caespitosa</i>	f	<i>C. flacca</i>	f
* <i>Prunella vulgaris</i>	f	<i>C. flavâ</i>	f
<i>Littorella lacustris</i>	o	* <i>Rhacomitrium heterostichum</i>	f
<i>Polygonum Hydropiper</i>	o	* <i>Climacium dendroides</i>	l
* <i>Juncus effusus</i>	f	* <i>Hypnum cuspidatum</i>	r

The species asterisked are characteristic of exposed places. The substratum is always stable, though wave washed when the water level is high. This community also passes into fen communities if peat or silt accumulates—the transition being marked by an abundance of *Agrostis alba*, *Molinia caerulea* and *Juncus sylvaticus*—and can be termed a *colony*, since it represents the invasion of a bare area by two or more species.

(iii) In many places, woods of *Quercus sessiliflora* extend almost to the water's edge. The slope is usually rather steep and the substratum of the same type as in the marginal colonies, which are confined to a narrow wave-washed zone near the water. Moisture-loving trees replace the oak along the water margin, and the ground flora beneath them is as follows, the trees themselves being *Fraxinus excelsior*, *Alnus rotundifolia*, and *Salix cinerea*, of which the alder is most abundant.

<i>Ranunculus Flammula</i>	f	<i>Achillea Ptarmica</i>	f
<i>R. repens</i>	o	<i>Senecio aquaticus</i>	o
<i>Caltha palustris</i>	f	<i>Onicis palustris</i>	l. ab
<i>Meconopsis cambrica</i>	r	<i>Centaurea nigra</i>	r
<i>Lychnis dioica</i>	f	<i>Scrophularia nodosa</i>	f
<i>L. Flos-cuculi</i>	f	<i>Rumex obtusifolius</i>	o
<i>Poterium officinale</i>	o	<i>R. acetosa</i>	l
<i>Spiraea Ulmaria</i>	ab	<i>Juncus articulatus</i>	o
<i>Lythrum Salicaria</i>	f	<i>J. sylvaticus</i>	ld
<i>Epilobium montanum</i>	o	<i>Phalaris arundinacea</i>	ld
<i>Circaea lutetiana</i>	o	<i>Agrostis alba</i> , v. <i>coarctata</i> Hoffm.	l
<i>Angelica sylvestris</i>	l. ab	<i>A. alba</i> , forma <i>gigantea</i>	l
<i>Galium Aparine</i>	o	<i>Deschampsia caespitosa</i>	l. ab
<i>Valeriana officinalis</i>	f	<i>Holcus lanatus</i>	o
<i>V. sambucifolia</i>	l	<i>Molinia caerulea</i>	ld
<i>Scabiosa Succisa</i>	ab	<i>Brachypodium sylvaticum</i>	l. ab

Nearer the water and light, *Phalaris* and *Juncus sylvaticus* are locally dominant; while further away *Molinia*, *Spiraea* and *Deschampsia caespitosa* become abundant, merging finally into damp oakwood with *Mercurialis perennis* and *Circaea lutetiana*. The inner marsh zone is distinguished from the outer by greater shelter, lower water table and weaker light intensity—

which falls from .5 to .05. Definite quantitative determinations of water and humus are not possible owing to the nature of the substratum: The slightly acid soil waters probably account for the presence of such species as *Molinia caerulea*, *Juncus sylvaticus*, *Rumex acetosa* and *Deschampsia caespitosa*. The two marsh zones are probably no more than societies (cf. Clements) of the oakwood community.

(iv) At the South end of the lake, there is a bank of morainic material, which, formerly submerged and superficially eroded, is now covered with vegetation. This bank has a maximum elevation of 2.75 m. above summer water level, a gradual slope—1 in 15—and its vegetation is divided into five well marked zones according to its distance from the water. At the water's edge, the gravel is unstable, and forms a slope about 1 m. wide, at the top of which a sparse marginal colony is developing. Pushing out on to this colony, *Carex elata* occupies the next zone, where the gravel is quite stable. During floods the *Carex* acts as a breakwater for the zones behind it, and normally affords a drier habitat for *Scabiosa Succisa*, *Caltha palustris*, *Lythrum Salicaria*, and *Valeriana sambucifolia*. The water level of the *Carex* zone varies between 7 and 14 cm. Behind this zone there is a dense sward, on stable gravel, of the following:

<i>Hydrocotyle vulgaris</i> f	<i>Juncus articulatus</i> l. ab
<i>Carex panicea</i> ab	<i>J. effusus</i> o
<i>C. echinata</i> f	<i>Prunella vulgaris</i> f
<i>Ranunculus repens</i> f	<i>Potentilla palustris</i> c
<i>R. Flammula</i> ab	<i>Lythrum Salicaria</i> f
<i>Viola palustris</i> f	<i>Molinia caerulea</i> f
<i>Spiraea Ulmaria</i> lf	

These are beyond the reach of wave wash, and as peat accumulates, *Molinia* and *Myrica Gale* extend downwards from the zone above, where they are dominant. The highest zone is a closed thicket of small trees:

<i>Betula tomentosa</i> ab	<i>Rhamnus frangula</i> f
<i>Salix cinerea</i> ab	<i>Coryllus avellana</i> l
<i>Alnus rotundifolia</i> ab	<i>Quercus sessiliflora</i> o
<i>Fraxinus excelsior</i> l	

This is extending on to the *Molinia-Myrica* zone, and will ultimately cover the lower zones as the water level gradually falls, owing to the cutting back of the outlet. It is a natural extension of an adjacent oakwood, and the respective zones will probably ultimately pass into oakwood societies akin to those described in (iii).

B. The Fen Successions. Fens at Esthwaite succeed the aquatic sere and are developed on peaty or sedimentary soils. The communities are described under this name because of their close floristic resemblance to those described in *Types of British Vegetation*. The fens at the north of the lake,

being most characteristic and instructive, will be considered first. Their development is chiefly due to the abundance of silt brought down by the Black Beck, of which the current is sufficient to transport stones to within 270 m. of the lake. Hence all the finer sediments, considerable in quantity, are dropped in the lake or in the fen round the beck mouth. In 1888, the lake water reached a point at least 25 m. further inland than it does today, giving an extension of almost 1 m. per annum. This rapid silting is in part due to the heavy annual rainfall, which at Esthwaite Mount was 71.3 ins. (175 cm.) for the period 1900-1909. At Black Fell, further up the valley, it was 81.3 ins. (200 cm.) during the same period. (*British Rainfall*.) Heavy rainfall and rapid silting are therefore, two of the conditions under which this fen has developed. Also important, probably, is the acidity of the waters of the stream, lake and fen soil—in reaction to phenol-phthalein.

Of these three factors, the deposition of sediment is most important. It is obvious that it will be most rapid round the beck mouth and will decrease to the right or left of the line of flow. This gives the clue to the conditions under which the fen soils are developed. Those along the stream side were built up rapidly of inorganic silt. Those furthest from it receive least silt and show a greater proportion of organic remains. Proceeding eastward from the Black Beck at A (see Fig. 9), the soils fall naturally into the three following types:

(1) Stations 4, 5, 6 and less typically 7. Soil light and grey brown in colour, clayey in texture. Ash at least 70 % of the whole, generally 75 to 80 %.

(2) Stations 8, 10 and 11. Black fen peat, amorphous, wet. Contains at least 40 % of ash.

• (3) Stations 15, 16, 17 and 18. Peat dark brown, and close textured, tough and fibrous, with plant remains well preserved. Less than 20 % of ash present.

Each of these three types of soil represents a zone in which the rate of sedimentation is approximately constant, and we are justified in distinguishing these, as respectively the zones of rapid, moderate and slow sedimentation.

Water level. The variations in water level in different parts of the fen were ascertained by digging holes at different stations, and after two days, taking readings on six successive days (Aug. 4th-9th, 1915), at the same time (2 P.M.) each day. The water levels were lowest near the stream, for the rapid sedimentation causes a distinct bank to develop along the stream side. The results are included in the descriptions of communities and their habitats, and, represented graphically, indicate three types of variation in the water level (Fig. 10).

Type 1. Holes at Stations 1, 2, 3 exemplify places where slight variations in water level correspond with the variations in lake level.

Type 2. In Stations like 4, 5, 6 and 7 the variations agree with those in the stream. These are all in the region of rapid silting.

Type 3. In these Stations (e.g. 15, 16, 17 and 18), the water levels apparently depend on locally varying factors, such as drainage and shelter. At the same time, rainfall causes a certain uniformity. These stations are those at some distance from the stream.

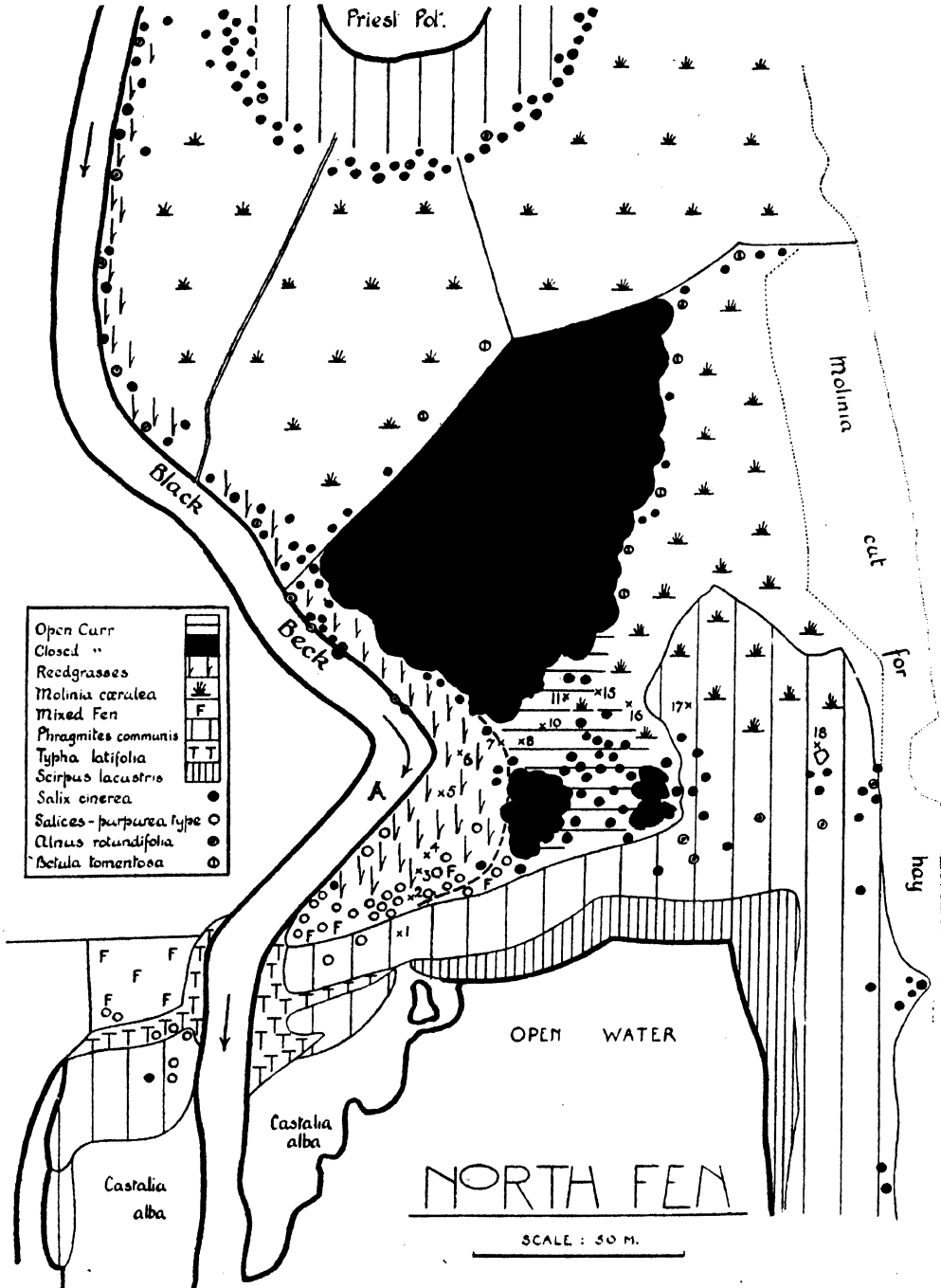


FIG. 9. Map of the fen plant communities on North Fen, Esthwaite Water.

The contrast between the two former types and the last is most clearly illustrated on August 9th. On that day, the stations of type 3 were drying up, and their water levels *falling*. The water levels of stations near the lake and stream were, on the other hand, *rising*, owing to the continued rise in lake and stream levels. Thus it seems reasonable to assume that there is an intimate connection between the soil water of the region of rapid sedimentation and the waters of the stream. The soil waters of places farther from the stream are chiefly renewed by rain water, but also by waters "banked up" from other parts of the fen.

We can now summarise the differences between the two extreme zones, as follows:

West of the Fen:

1. Soil inorganic and clayey.
2. Abundant inorganic silt.
3. Soil water dependent on that of the stream.
4. Soil level higher and relatively well drained.

East of the Fen:

1. Soil peaty and undecayed.
2. Little or no inorganic silt.
3. Water much more dependent on rain.
4. Soil level low, and drainage bad.

All the above factors are dependent on, and vary as, the rate of sedimentation, and therefore, in subsequently referring to the rate of sedimentation, the other conditions will be implied.

Before describing the plant communities on these types of substratum, the methods used may be briefly described: light intensity was determined in some cases by the iodine method (described above); in the remaining instances by a photographic actinometer.

Soil samples were estimated in accordance with Crump's method (4).

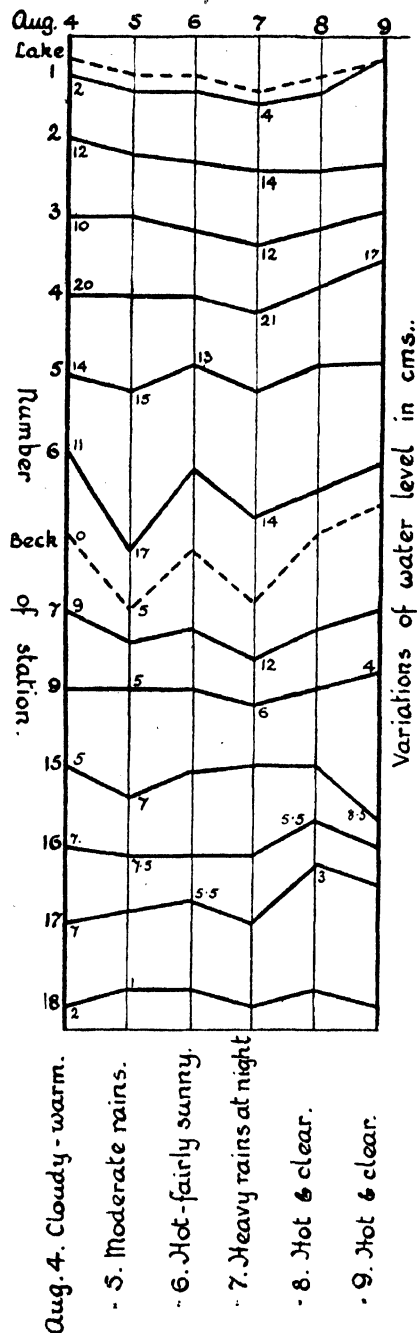


FIG. 10. Variations in water level in North Fen in the neighbourhood of the Black Beck, on successive days in August, 1915.

Water, humus and ash contents are expressed as percentages of the *air-dried soil*, the coefficient of soil humidity then being found from: $\frac{\text{water content}}{\text{humus content}}$.

Owing to the frequent rains in a region of high rainfall the coefficient of relative humidity is of rough comparative use only, and the position of the water table is as a rule, of greater value in estimating soil humidity at Esthwaite.

The plant communities on this fen are related to the variations in conditions described above, for each of the zones of sedimentation is characterised by a distinct belt of vegetation. Even the reedswamp, common to all three zones, shews considerable variations in the different zones. Taken in order from the lake inland, the typical communities of each of the three silting areas are as follows:

1. Area of Rapid Sedimentation.

(i) Reedswamp. (ii) Mixed fen associes. (iii) Reedgrass associes.

2. Area of Moderate Sedimentation.

(i) Reedswamp. (ii) *Carex elata* consocies. (iii) Open carr. (iv) Closed carr.

3. Area of Slow Sedimentation.

(i) Reedswamp. (ii) Transition communities. (iii) *Molinia caerulea* consocies.

In each zone, the communities succeed one another in the order given, as the peat level gets higher, and the substratum becomes older. The inter-relationships of the three successions will be indicated later.

1. **Area of Rapid Sedimentation.** Though in this zone the substratum is typically inorganic, the two earlier communities occur on relatively organic soils, due to the vast accumulations of organic debris from the annual dying down of the rich reedswamps—in places over 4 m. high. The following soil samples shew this and indicate the edaphic conditions of the different communities.

Community	Humus Content (%)	Ash Content (%)	Water Level
(i) Reedswamp	55.9	34.2	0-12.5 cm.
"	47.8	42.9	
"	52.8	38.5	
"	54.5	41.4	
(ii) Mixed fen associes	54.6	38.8	10-15 cm.*
" "	49.4	40.9	
" "	37.3	53.5	
(iii) Reedgrass associes	19.1	77.4	10-30 cm.*
" "	16.6	79.6	
" "	24.0	71.8	

* Water level does not distinguish between these communities, as between Reedswamp and Mixed Fen. In the case of the mixed fen and reedgrass associes, the ratio of inorganic to organic matter seems to be the important distinguishing factor.

(i) The reedswamps in this zone are peculiar in the absence of *Scirpus lacustris*, the presence of *Typha latifolia* and the abundance of herbaceous

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species. *Typha* replaces *Phragmites* on both sides of the stream, and is also abundant along the inside of the reedswamp. The chief associates of the two dominants are *Scutellaria galericulata*, *Menyanthes trifoliata*, *Caltha palustris*, and *Ranunculus Lingua*, but most of the species in the mixed fen are occasionally found. Yapp (17) has shewn the importance of shelter and shade to such plants, and here they occur in a light intensity of less than .25. The peat is nearly black on the surface and contains an average of 52.75 % organic content. The water level varies from .9 m. above the surface to 12.5 cm. below it.

(ii) The mixed fen associates, which succeeds reedswamp in this zone, is characterised by its number of co-abundant species and its consequent richness of aspect. The following plants are most typical:

Locally dominant or sub-dominant.

<i>Typha latifolia</i>	<i>Iris Pseudacorus</i>
<i>Phalaris arundinacea</i>	<i>Carex elata</i>
<i>Menyanthes trifoliata</i>	<i>Galium palustre</i> .

Abundant or locally so.

<i>Ranunculus Lingua</i>	<i>Menyanthes trifoliata</i>
<i>Lotus uliginosus</i>	<i>Phragmites communis</i>
<i>Spiraea Ulmaria</i>	<i>Agrostis alba</i> var. <i>major</i>
<i>Potentilla palustris</i>	<i>Carex inflata</i>
<i>Lythrum Salicaria</i>	<i>Salix purpurea</i>
<i>Lysimachia vulgaris</i>	<i>Salix cinerea</i> sub-sp. <i>aquatica</i>
<i>Myosotis palustris</i>	<i>Salix decipiens</i> Hoffm.

Salix purpurea and *S. decipiens* are particularly characteristic of regions of rapid sedimentation, and are accordingly distinguished on the maps. The associates is well developed to the West of the Black Beck and as a rather narrow zone to its East. While the soil is black and muddy, the abundant silt and less rank vegetation cause a fall in the organic content which averages 47.1 %. In winter the soil is submerged, but in summer the water level is from 10–15 cm. below the surface, about the usual level of the reedswamp remains.

(iii) The reedgrass associates includes consociates of *Phalaris arundinacea*, *Spiraea Ulmaria*, and *Calamagrostis lanceolata*, of which the first occurs in the lowest parts nearest the lake, and the last favours the older, drier parts of this zone of rapid silting. Though these consociates are typically pure, the following associates may also occur:

<i>Caltha palustris</i>	If	<i>Urtica dioica</i>	o
<i>Galium palustre</i>	If	<i>Valeriana officinalis</i>	l
<i>Juncus effusus</i>	o	<i>Salix cinerea</i>	l
<i>Scutellaria galericulata</i>	o	<i>S. decipiens</i>	l

The associates always occurs on grey-brown clayey silt, having an average humus content of only 20 % (ash, 76 %), and this is the most characteristic edaphic condition, though the water level, ranging from 10–30 cm., is generally well below that of the mixed fen. All that has been said of the region of rapid sedimentation applies particularly to the habitat of this associates.

Fringing the stream, though not strictly members of this community, *Alnus glutinosa*, var. *microcarpa* and *Sparganium neglectum*, are found.

2. Area of Moderate Sedimentation.

(i) The reedswamps here differ from those of the area of rapid sedimentation in the absence of *Typha latifolia* and the sparsity of herbaceous associates, for *Ranunculus Lingua* is rare, and *Menyanthes trifoliata* is the only common herbaceous species. Another difference is the dominance of *Scirpus lacustris* towards the water, *Phragmites communis* being confined to the landward parts. The peaty substratum is also closer and tougher, and has slightly higher average organic content.

(ii) The *Carex elata* consociates succeeds the reeds, and has the following composition:

<i>Carex elata</i>	d	<i>Hydrocotyle vulgaris</i>	o
<i>C. vesicaria</i>	l. sd	<i>Scutellaria galericulata</i>	f
<i>C. inflata</i>	l	<i>Phalaris arundinacea</i>	l
<i>Lythrum Salicaria</i>	f	<i>Phragmites communis</i>	f
<i>Galium palustre</i>	f	<i>Typha latifolia</i>	r
<i>Potentilla palustris</i>	f	<i>Eriophorum angustifolium</i>	r
<i>Senecio aquaticus</i>	l		

In position this *Carex* zone corresponds closely to the mixed fen, though differing so much from it in floristic composition. The water level is from 5 to 10 cm. below the surface and in no case does *Carex elata* remain dominant after the water level has fallen to a depth of 15 cm. The soil is essentially the same as in the preceding reedswamp, and contains 55 % (average) of humus. The greater closeness of the soil and its rather brown colour, however, indicate a considerable difference in nature from the soils of the mixed fen.

(iii) **Open carr** succeeds the *Carex* community, when *Alnus glutinosa* and *Salix cinerea* become sub-dominant; *S. purpurea* is frequent (a) near the lake, (b) near the zone of rapid sedimentation. The ground flora includes almost every species found on these fens, but lacks a clearly defined dominant, and merges into that of the surrounding communities. Though intermediate in composition and position, open carr is nevertheless extensive and quite distinct in appearance.

The full list of species is as follows:

<i>Ranunculus repens</i>		<i>Viola palustris</i>	f
<i>Caltha palustris</i>	f	<i>V. canina</i>	
<i>Cardamine palustris</i>		<i>Lychnis Flos-cuculi</i>	l

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<i>Stellaria palustris</i>		<i>R. crispus</i>	
<i>Lotus uliginosus</i>	f	<i>R. acetosa</i>	
<i>Lathyrus pratensis</i>		<i>Urtica dioica</i>	
<i>Spiraea Ulmaria</i>	ab	<i>Orchis maculata</i>	
<i>Potentilla palustris</i>	f	<i>Iris Pseudacorus</i>	f
<i>Poterium officinale</i>		<i>Juncus effusus</i>	f
<i>Parnassia palustris</i>		<i>J. articulatus</i>	
<i>Lythrum Salicaria</i>	l. ab	<i>J. sylvaticus</i>	l. ab
<i>Epilobium parviflorum</i>		<i>Eleocharis palustris</i>	
<i>Hydrocotyle vulgaris</i>	f	<i>Carex paniculata</i>	l. ab
<i>Angelica sylvestris</i>	f	<i>C. curta</i>	
<i>Galium palustris</i>	f	<i>C. elata</i>	f
<i>Valeriana officinalis</i>	f	<i>C. Goodenowii</i> var. <i>juncella</i>	
<i>V. sambucifolia</i>	f	<i>C. panicea</i>	
<i>Scabiosa Succisa</i>	f	<i>C. inflata</i>	f
<i>Achillea Ptarmica</i>	f	<i>C. vesicaria</i>	f
<i>Senecio aquaticus</i>		<i>Phalaris arundinacea</i>	l. ab
<i>Cnicus palustris</i>		<i>Anthoxanthum odoratum</i>	
<i>Centaurea nigra</i>		<i>Phleum pratense</i>	
<i>Crepis paludosa</i>	l	<i>Agrostis alba</i>	l. ab
<i>Lysimachia vulgaris</i>	l	<i>A. vulgaris</i>	
<i>Menyanthes trifoliata</i>	f	<i>Deschampsia caespitosa</i>	l. ab
<i>Myosotis scorpioides</i>		<i>Holcus lanatus</i>	
<i>Solanum Dulcamara</i>		<i>Phragmites communis</i>	
<i>Scrophularia nodosa</i>		<i>Molinia caerulea</i>	ab
<i>Veronica scutellaria</i>		<i>Lastraea spinulosa</i>	
<i>Mentha arvensis</i>		<i>Equisetum limosum</i>	
<i>M. aquatica</i>			
<i>Lycopus europaeus</i>		<i>Salix cinerea</i>	ab
<i>Scutellaria galericulata</i>		<i>Betula tomentosa</i>	l
<i>Prunella vulgaris</i>		<i>Viburnum Opulus</i>	o
<i>Stachys palustris</i>		<i>Salix purpurea</i>	l. ab
<i>S. palustris</i> var. <i>canescens</i>		<i>Rosa coriifolia</i>	o
<i>Galeopsis Tetrahit</i>		<i>Rubus Idaeus</i>	l
<i>Rumex obtusifolius</i>		<i>Alnus glutinosa</i>	f

The most widely distributed of the above plants is *Molinia caerulea*, though it is not most abundant; as a rule, the variations in the trees coincide most closely with the changes in water and humus content; *Salix purpurea* on the drier, more inorganic soils, and *Betula tomentosa* where the organic content is very high. *S. cinerea* is intermediate in this respect.

The soil samples taken from open carr will be found in the appendix (Series I, II and III). The remarkable range in the coefficient of soil humidity

(6 to 12, at least) and in the water level (from the surface to 15 cm. below), indicates that neither of these is a determining factor for this community. The same is probably true of the organic content, which ranges from 30–75 %. The nature of the soil waters is, however, probably uniform, for all the more organic of the samples come from stations of low level, frequently flushed by relatively silt-free waters. The less organic samples come from situations where silting has been abundant, but is now infrequent, owing to the higher level of the fen. The soil in these cases accomplishes what the frequent flushings of the more organic situations ensure.

The trees in open carr tend to form closed thickets and finally to develop into closed carr, as on the East Anglian fens (see **14**, p. 236), to which these communities shew the greatest similarity.

(iv) **Closed carr** is very extensive on the North Fen (Fig. 9), and also as a thick belt round Out Dubs Tarn (Fig. 11). *Salix cinerea* is dominant, and the other trees found in open carr are rare. The trees are close together and the canopy dense, so that the light seems dim. Combined with the sparsity of the ground flora, the uniform brown mud along with the grey willow stems gives an impression of intense monotony. The list of species is as follows:

TREES:

<i>Salix cinerea</i>	d	<i>Rhamnus frangula</i>	l
<i>S. aurita</i>	r	<i>Betula tomentosa</i>	l
<i>S. purpurea</i>	r	<i>Myrica Gale</i>	o
<i>Alnus rotundifolia</i>	l		

HERBS:

<i>Calltha palustris</i>	l	<i>Scutellaria galericulata</i>	o
<i>Ranunculus Flammula</i>	l	<i>Iris Pseudacorus</i>	l
<i>Spiraea Ulmaria</i>	l. ab	<i>Carex vesicaria</i>	f
<i>Potentilla palustris</i>	o	<i>C. elata</i>	l. ab
<i>Lythrum Salicaria</i>	f	<i>Agrostis alba</i> var. <i>major</i> (Gaud.)	l
<i>Galium palustre</i>	o	<i>Phragmites communis</i>	l. ab
<i>Valeriana sambucifolia</i>	o	<i>Molinia caerulea</i> var. <i>viridiflora</i>	l. ab
<i>Mentha arvensis</i>	l		

Mosses and liverworts are characteristic, though the species are few:

<i>Amblystegium serpens</i>	l. ab	<i>Fissidens taxifolius</i>	f
<i>Mnium punctatum</i>	f	<i>Hypnum Patientiae</i>	o
<i>Plagiothecium denticulatum</i>	f	<i>Lophocolea bidentata</i>	f
<i>Pterygophyllum lucens</i>	o	<i>Plagiochila asplenoides</i>	l

Most of these species follow the outer edges of the wood. The *Carices*, *Phragmites* and *Iris* are nearly always non-flowering. *C. elata* is characteristic of the damper places nearer the open water, *Molinia* of those areas furthest away, while the local communities of *Phragmites* tend to occur in slight depressions.

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The soil though shewing the same two types on analysis as open carr, is always clayey in texture and brown in colour (see Appendix, Series IV and V).

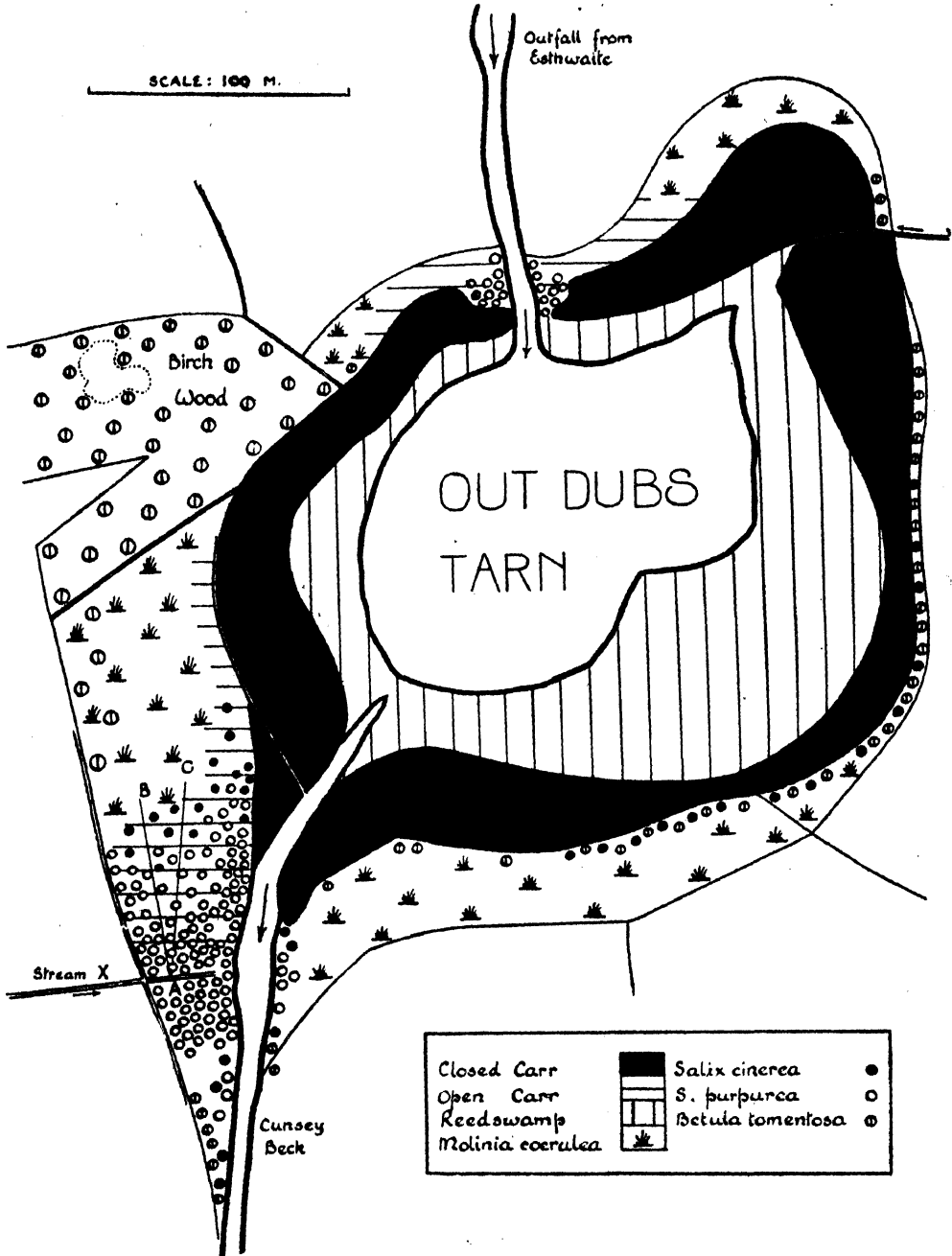


FIG. 11. Fen communities round Out Dubs Tarn, South of Esthwaite Water.

The organic content is higher, ranging from 40 to 75 %, and the variability less striking. The water level is rather more (5 to 20 cm.), but the drainage is very bad, and it is very common to find soil and water levels coinciding,

after light rains, although the soil surface is higher. The close soil and the complete shelter probably account for this. The factor which distinguishes open from closed carr seems probably to be the greater rate of deposition of silt in the former. Combined with low level, this may be unfavourable to tree growth. Thus on the North Fen and near stream X at Out Dubs, silting has been heavy but is now almost arrested, where open carr is developed. But round most of Out Dubs Tarn, silt comes only from the lake waters—already filtered in Esthwaite and again by the extensive reedswamp—and so silting has been, and is, slight. Here *closed carr* immediately succeeds *Carex elata*. Rapid silting in open carr has probably a physical effect—the instability and rapid raising of the substratum—for at Hawes Water (W. Lancs.) and Woodwalton Fen (Hunts.), closed carr immediately follows reedswamp, though in each case the chemical result of rapid silting (quick decomposition of humus) is ensured by the richness of the soil waters in calcium carbonate.

It is almost certain that light intensity limits the ground flora, for where trees have fallen, and the light intensity rises as high as $\cdot 7$, there is a dense local vegetation of *Spiraea Ulmaria*, *Carex elata* and *Lythrum Salicaria*, all flowering. In old carr the light intensity averages $\cdot 032$ (range $\cdot 01$ to $\cdot 05$) and ground flora is practically absent. The usual sparse ground flora occurs where light intensity is $\cdot 1$ (range $\cdot 03$ to $\cdot 14$). To avoid reeds, all the above readings were taken $\cdot 9$ m. above the ground.

In Gamlingay Wood (Adamson, 1) *Spiraea Ulmaria* is dominant under light intensities of $\cdot 005$ to $\cdot 01$, on soil with a water content of 36–43 % (of wet soil). The water content of the wet soil in carr is between 80–90 %, and hence apparently *Spiraea* needs a higher light intensity on wet, ill-drained soils like this, than on drier ones.

Carr at Esthwaite never shews any seedlings or young willows and apparently does not regenerate itself.

3. **Area of Slow Sedimentation.** In this zone, the description of communities really resolves itself into an account of the habitats of two plants, *Phragmites communis* and *Molinia caerulea*. While the former is, as usual, characteristic of the reedswamp, it also extends some 45–50 m. inland as a subdominant, after which it dies down and is totally replaced by *Molinia*. The reedswamp here is very similar to that of the area of moderate sedimentation, but the peat is still closer and less decayed, and has a higher average organic content of 59.1 % (see Appendix, Series VI). As the *Phragmites* becomes less abundant, *Potentilla palustris* becomes abundant or subdominant, and *Carex inflata* and *Lysimachia Nummularia* are frequent. The light intensity is here about $\cdot 2$ to $\cdot 3$ and the soil peaty and muddy.

The *Molinia* consociates only gradually ousts *Phragmites*—owing to the very gradual raising of the soil level. The transition zone is some 25 m. wide, *Molinia* apparently becoming co-dominant as the light intensity

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exceeds .4, and replacing *Phragmites* completely as the water level gets further below the surface. Thus while *Phragmites* tends to be more abundant where the water level is about 2.5 cm. below the surface, *Molinia* tends to be dominant where the water is at a depth of 10 cm.

Besides succeeding reedswamp in this way, the *Molinia* consociates also develops in succession to carr. It is then further from the open water, i.e. from silt (see maps), and in places shews stumps of dead trees, e.g. south of Out Dubs. The peat below such *Molinia* always contains a wood layer in which *Betula* is frequent at the top, and the less preserved remains of *Salix* usually abundant below, in clayey peat corresponding to that of carr.

Thus there are two types of *Molinia* consociates, developed respectively from reedswamp and carr. These two types are floristically the same, and probably similar in habitat. The following species occur in this consociates:

<i>Potentilla erecta</i> l	<i>Pyrus aucuparia</i>	o
<i>Galium saxatile</i> f	<i>Myrica Gale</i>	l. sd
<i>Scabiosa Succisa</i> l	<i>Salix cinerea</i>	o
<i>Lastraea aristata</i> r	<i>Betula tomentosa</i>	l. ab
<i>Molinia caerulea</i> d	<i>Sphagnum acutifolium</i> (agg.) l	

Of these species *P. aucuparia* and *Betula tomentosa* are confined to drier, usually drained places, and *Salix cinerea* to the damp edges near the preceding communities.

The summer water level is near the surface (7–15 cm.), where the consociates develops from reedswamp, but falls from this to 37 cm. where carr is the preceding community. As might be expected, the soils fall into two well-marked classes (see Appendix, Series VII and VIII):

1. Developed from reedswamp. Humus content (mean), 68 %; Ash, 23 %; Coefficient of humidity, 9–15.

2. Developed from carr. Humus content (mean), 84.8 %; Ash, 6.1 %; Coefficient of humidity, 6–9.

Thus this consociates apparently develops (cf. carr) under two sets of edaphic conditions. The lower habitat has a greater ash content consequent upon its frequent flushings, but is wet and ill-aerated. The higher habitat has a very low ash content, is only occasionally flushed, but is drier and much better aerated. The soil waters are, therefore, probably similar, and humus content and water content have probably, in this instance, a certain edaphic equivalence.

In comparison with the other fen habitats, these soils are remarkable for their high organic content, due to the paucity of silt. Flood waters on these soils are chiefly composed of water “banked up” from stations nearer the lake, and from which most of the bases are already adsorbed. Moreover, the water level has been shewn to fluctuate rather in accordance with rainfall, than with variations in stream or lake levels. Four factors then, exist which

tend to prevent the decay of humus, and conversely, favour the development of soil "acidity": (1) paucity or absence of silt, (2) waters atmospheric or denuded of bases, (3) high humus content, (4) acid lake waters.

It seems, therefore, doubtful if we can rank the *Molinia* consociates as a fen community, since the characteristic of fens, *carr*, is not developed on it, and it has all the concomitants of soil "acidity." Nevertheless, owing to its relation to the fen type of vegetation, and to the fact that it may be frequently, and is, apparently, always occasionally flushed, it is difficult to consider this consociate as belonging to the moor types of vegetation. I therefore propose to distinguish such intermediate communities as *bogs*, differing from *marsh* by their development from aquatic vegetation, and from *fen* by their soil "acidity" and the absence of *carr*. From *moor*, they differ in not being entirely dependent on atmospheric precipitation.

The fact that the *Molinia* consociate needs greater humus and water contents in the soil, than do other fen communities, is illustrated by the soil samples in Series I (see Appendix). Of the four stations where *Molinia* is dominant or nearly so, 64 and 71 have very high water content, 65 has a high humus content, and in 69 both water and humus are above the average. These samples were taken along the line *AB* at Out Dubs Tarn. The samples in Series II were taken along the line *AC*, and illustrate the same point more fully. They fall into the following groups (in brackets in App.):

1. *Salix purpurea* sd. No *Molinia*. Average Soil Humidity, 4.6; Average Humus Content, 35.2 %.

2. *S. purpurea* f. or ab., *Molinia* f. or ab.: Average Soil Humidity, 6.06; Average Humus Content, 42.0 %.

3. No *S. purpurea*, *Molinia* sd.: Average Soil Humidity, 7.6; Average Humus Content, 43.6 %.

It is also interesting to notice the high soil humidity of the *Molinia* habitat, which is farthest from open water.

The *Molinia* consociate includes other caespitose plants, where it passes into closed or open *carr*, and in such places *Deschampsia caespitosa*, *Carex paniculata* and *Juncus sylvaticus* may occur abundantly. In habitat and composition such a *societas* bears considerable resemblance to the "stooled meadow" type of grassland described by Smith and Crampton (13), and considered by them to be an adaptation to gentle flooding and silting, in positions where scouring by water currents is prevented.

Where the peat of the *Molinia* consociate is drained, *Betula tomentosa* becomes frequent, and west of Out Dubs Tarn this has developed into a Birch-wood, though such woods do not apparently occur normally. The wood at Out Dubs is shewn on the 1888 6 in. O.S., but is now much more extensive, and it includes the following species:

<i>Betula tomentosa</i>	d	<i>Rhamnus frangula</i>	1
<i>Pyrus aucuparia</i>	o	* <i>Myrica Gale</i>	o

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* <i>Viola palustris</i>	l	<i>C. echinata</i>	o
<i>Galium saxatile</i>	ab	<i>Molinia caerulea</i>	l. ab
* <i>G. palustre</i>	o	* <i>M. viridiflora</i>	f
<i>Oxalis acetosella</i>	o	<i>Anthoxanthum odoratum</i>	f
<i>Potentilla erecta</i>	f	* <i>Agrostis alba</i>	l
<i>Rubus fissus</i>	ab	<i>A. tenuis</i>	f
<i>R. Idaeus</i>	l	<i>Holcus mollis</i>	o
<i>Scabiosa Succisa</i>	l. ab	<i>Athyrium Filix-foemina</i>	o
* <i>Hydrocotyle vulgaris</i>	l	<i>Lastraea aristata</i>	o
* <i>Cnicus palustris</i>	l	<i>Pteris aquilina</i>	o
<i>Digitalis purpurea</i>	f	<i>Mnium hornum</i>	f
<i>Rumex acetosa</i>	f	<i>Polytrichum commune</i>	f
<i>R. acetosella</i>	l. ab	* <i>Sphagnum</i> sp.	l
* <i>Juncus effusus</i>	l	<i>Lophocolea bidentata</i>	f
<i>Luzula multiflora</i>	o	<i>Plagiothecium</i> sp.	l
<i>Carex panicea</i>	o		

Of these species, those asterisked occur in damper places, either toward the carr, or where the peat has sunk, the water level being then at a depth of 5–25 cm. In all the intermediate stations in the wood, *Galium saxatile* is the only abundant plant, light intensity .1 to .3. Towards the drier margins of the wood, *Rubus fissus* is dominant, with a light intensity exceeding .15. If the light intensity exceeds .4, *Molinia* becomes dominant, and towards the lowest range of light intensity, .02, there is little vegetation except mosses.

The whole wood is developed on deep peat, with the water level typically from 40 to 62 cm. below the surface. Under the wettest flood conditions, this level rarely rises to within 25 cm. of the surface. The peat is almost black, and quite amorphous, and its composition at greater depths indicates that it represents a phase of *Molinia* long continued. The peat composition is well represented by the Series VIII, except that the soil humidity is between 5 and 6.

VI. THE RELATION OF ESTHWAITE FENS TO MOOR

The abundance of lowland moors of estuarine and lacustrine origin in the neighbourhood of Esthwaite Lake (see map of district, Fig. 1, *Journ. of Ecol.*, 5, p. 181), suggests the possibility that the Esthwaite fens may pass into moors of this type. The acid soil waters, high rainfall and the presence of some moor plants (e.g. *Sphagnum*) shew that some of the necessary conditions are present at Esthwaite. At Rusland, some six miles (9.6 km.) slightly West of South (see Fig. 1), there is an extensive lacustrine moor, lying on the same strata as Esthwaite and with almost identical drainage water, viz. Total residue, .07 grams per litre; Mineral residue, .052 grams per litre; compared with .072 and .041 for Esthwaite. The Rusland Pool

also brings down much similar sediment in flood, and its waters are acid in reaction.

The vegetation of Rusland Moss (see Fig. 12) is essentially similar to that

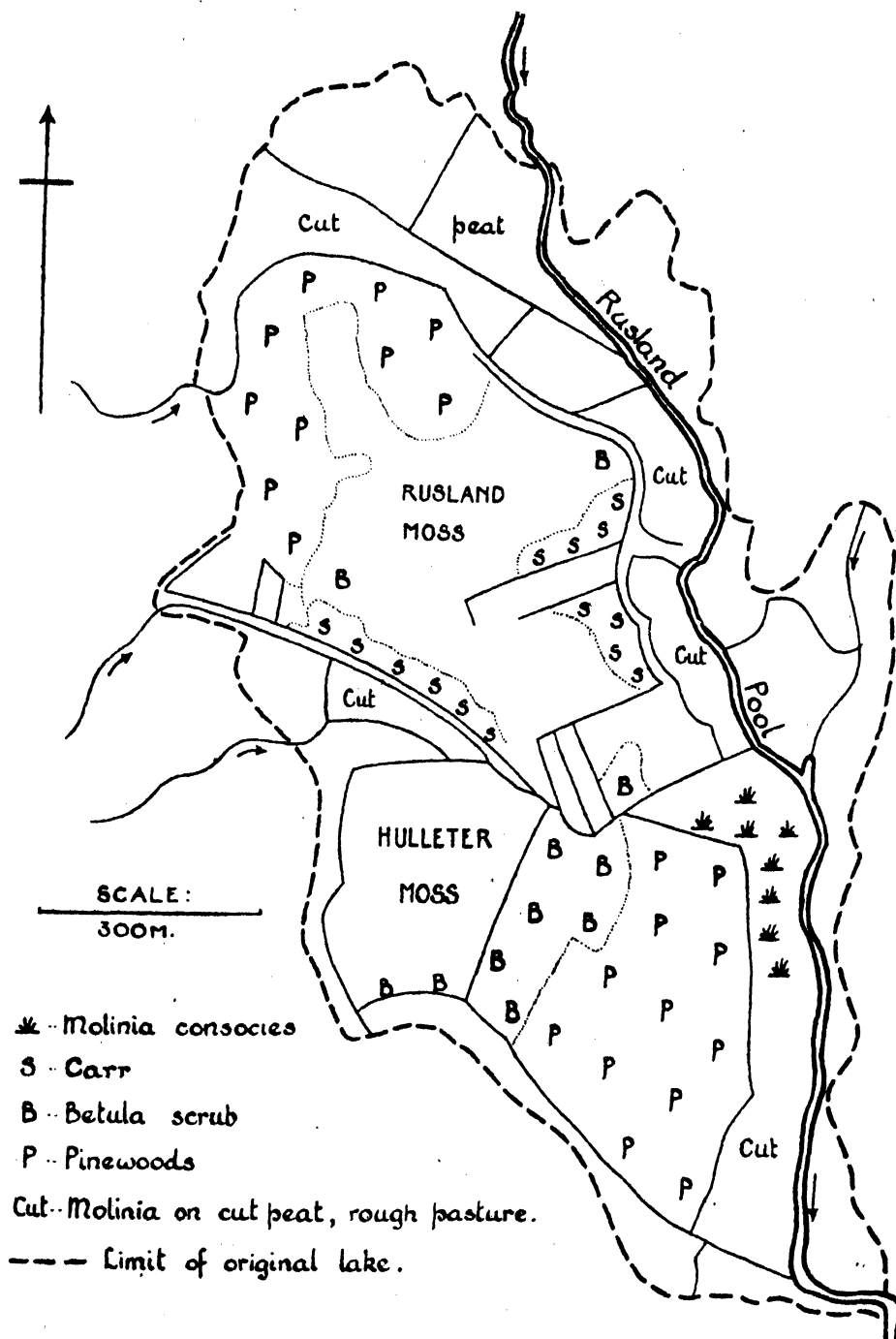


FIG. 12. Map of the plant communities round Rusland Moss.

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described by Rankin¹, but the moss is much cut, locally planted with *Pinus sylvestris*, and traversed by small drainage streams. Fringing these streams and also the Pool, are communities of a strikingly different type—in part vestigial, and in part restored by the influence of the fresh waters on the peat, lowered by cutting. Thus, between the Pool and the *Pinus* plantation, a community of the following composition is developed:

<i>Molinia caerulea</i> d	<i>Scabiosa Succisa</i> f
<i>Myrica Gale</i> l. ab	<i>Potentilla erecta</i> f
<i>Betula tomentosa</i> lf	<i>Sphagnum acutifolium</i> f
<i>Salix cinerea</i> o	<i>Cirsium palustre</i> o

and nearer the water the following also appear:

<i>Angelica sylvestris</i> f	<i>Valeriana sambucifolia</i> f
<i>Juncus sylvaticus</i> f	<i>Rhamnus frangula</i> o
<i>Lythrum Salicaria</i> o	

There seems no reason to doubt that this community is the *Molinia* consocieties already described, for it corresponds in water level and soil type most exactly. Owing to the Pine plantation behind it, no clue can be gathered as to how it passes into moor. The adjacent meadows, on drained peat, are also dominated by *Molinia*, but are floristically modified through being cut for hay.

In many places, where the peat level has been reduced almost to the water level, *Salix cinerea* is dominant in clumps, with open patches between them. These exactly resemble in appearance, floristic and edaphic characters, the open and closed carr at Esthwaite. Silt is deposited in small quantities by floods. It is thus clear that both similar climatic and edaphic conditions, and similar plant communities, indicate that this moor has developed from fens of the Esthwaite type, and this conclusion is further borne out by an examination of the peat layers.

Underneath the surface *Sphagnum* peat, at varying depths, between 1.5 and 3 m., there is a layer of dark brown peat, with an ash content of 2.6–3.1 %. It contains twigs of *Calluna*, *Sphagnum* remains in pockets, *Betula* wood rather locally, and flattened fibrous tufts of a grass-like plant, in large quantities. It probably represents a long phase with *Molinia* dominant, for the ash content is too high for *Sphagnum* peat and the peat resembles that from an old *Molinietum* at Esthwaite—ash content 3.5 to 4.5 %—containing grass tufts of the same sort. This layer overlies (cf. Esthwaite) a wood layer of about 20–30 cm. in thickness, chiefly composed of *Betula*, with hardly recognisable, abundant remains of *Salix* and *Alder* below. The wood, often upright and rooted, has occasionally been cut. This layer seems to correspond with carr remains. Clayey peat, often humus stained to 3.1 m., is found immediately below, containing *Phragmites*, *Typha*, *Equisetum limosum*, *Carex*

¹ In *Types of British Vegetation* (pp. 247 to 259).

spp., and skeleton leaves, apparently of a *Salix*. The basement clay is identical with that of Esthwaite.

Thus we may conclude that this moor has passed through essentially the same succession as is now exemplified at Esthwaite. Why then are not the Esthwaite communities passing into moor? The answer is because the Esthwaite basin is long and narrow. Rusland lake was broad and shallow, and the prevalent winds drifted the stream waters to the east (see Fig. 12), so that there was a very extensive area of slight sedimentation to the west, possessing all the characters of the similar area on North Fen. The centre of this area had all the conditions necessary for moor formation—absence of silt, dependence on aerial waters, deficient drainage, high humus content and heavy rainfall. As the peat got above flood level, the *Molinia* consociates would gradually pass into moor communities, as indicated by the *Sphagnum* and *Calluna* remains in the peat.

I believe that the preceding descriptions exemplify what has long been known from peat remains, that lowland moors represent the final stages of one long succession of plant communities, starting in bare stones or mud, and passing through aquatic and fen stages, before becoming stable. I have already proposed that all this be termed the *moor* formation, and in this I adopt Clements' definition of the formation as delimited by climate (2), and apply his nomenclature to the constituent communities. That moor can be regarded as a climatic formation, is proved by its permanence in the western parts of the British Isles. Both present observations and the peat evidence shew that the hydrarch succession does not, as in the U.S.A., pass into forest. The present types of wood which may occur on lowland moors in the Lake District are three in number:

1. Sub-spontaneous or planted woods of *Pinus sylvestris* are frequent, but only where the peat has been cut or drained. These processes produce a rather loose surface of open peat, which facilitates the oxidation of the humus present, and the peat becomes dry, amorphous, and relatively well aerated—all conditions lacking in normal moor peat.

2. *Betula* scrubs or woods are frequent round the margins of lowland moors, but in all cases I have observed are due to drainage, when the same conditions follow as above, though less completely.

3. Alder (*Alnus*) or *Salix* woods occur as marginal zones or when the peat is cut so low as to allow flushing by stream waters. In neither case can moor conditions be said to hold.

Hence lowland moors do not naturally produce woodland under present climatic conditions. Since further, moor peat shews only local wood layers corresponding to the types of wood already described (cf. also *Types*, 14, p. 253), we are fully justified in adopting *moor* as the formational name for this biotic succession.

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SUMMARY OF ESTHWAITE FEN SUCCESSIONS.

Rate of Sedimentation.

	Rapid	Moderate	Slow	None
1.	<i>Typha latifolia</i> consocieties 50	<i>Scirpus lacustris</i> consocieties 55		
2.	<i>Phragmites</i> consocieties	<i>Phragmites</i> consocieties	<i>Phragmites</i> consocieties 60	
3.	Mixed Fen associates 47	<i>Carex elata</i> consocieties 55		
		Open Carr	Transitional communities	
4.	Reedgrass associates 20	<i>S. purpurea</i> Soils inor- ganic 38. Silt- ing occasional <i>S. cinerea</i> Soils often flushed by silt- free water 65		
5.		Closed Carr	<i>Molinia caerulea</i> con- societies 85	<i>Betula</i> wood, if drained, 85 Moor, normally + 90
		Soils as above 45	Soils as above 70	

APPENDIX: *Soil Samples.*

Series I

	Number of Sample	Community	Water Content	Coefficient of Soil Humidity	Humus Content	Ash Content
Open Carr	60	<i>Salix purpurea</i> sd.,	279	7.5	37.3	53.5
	61	<i>Rubus Idaeus</i> ,	209	6.9	30	60.5
	62	<i>Juncus sylvaticus</i>	202	6.4	31.7	59.1
	63		168.6	6.0	28	63.0
	64	<i>Molinia</i> sd.,	415.4	9.2	44.8	46.8
	65	<i>J. sylvaticus</i> ab.	352	6.0	58.7	33.4
	66	<i>Salix purpurea</i> lab.,	313	6.7	46.7	43.5
	67	<i>S. cinerea</i> lab.,	282	6.6	42.8	48.5
	68	<i>Rubus fissus</i> ,	274	6.4	43.0	48.5
	69	<i>Molinia</i> ,	372	7.1	52.3	37.7
	70	<i>J. sylvaticus</i>	216	6.5	33.3	58.0
	71	<i>Molinia</i> d.	265	8.1	32.5	59.0

Series II

Open Carr	29	<i>S. purpurea</i> d.,	143	4	35.7	56
	30	<i>J. sylvaticus</i> ,	128.2	4.27	30	64.2
	31	<i>Phalaris</i> , <i>Spiraea</i>	221.4	5.5	40	50.9
	32	<i>S. purpurea</i> ab.,	215	6.16	34.9	57.4
	33	<i>Angelica sylvestris</i> ,	323	6.1	53	37.5
	34	<i>Spiraea</i> ,	247.1	5.9	41.8	48.6
	35	<i>J. sylvaticus</i> ,	284.3	6.26	45.3	44.7
	36	<i>Molinia</i>	203.1	5.9	34.6	56
	37	<i>Molinia</i> sd., <i>Carex</i>	135.6	7.4	18.2*	77
	38	<i>paniculata</i> , <i>Des-</i>	268.6	6.7	40	50.5
	39	<i>champsia caespitosa</i> ,	410.6	8.2	45.2	40.5
	40	<i>Salix cinerea</i>	368.0	8.0	45.7	43.6

* Many small stones present.

Series III

	Number of Sample	Community	Water Content	Coefficient of Soil Humidity	Humus Content	Ash Content
Open Carr	72	<i>Salix cinerea</i> ab.,	825	11	75	11.3
	73	<i>Molinia</i> ab. to sd.,	800	11.9	67	24.3
	74	North Fen.	720	10.3	70	19.1
	26	Same, Out Dubs	528	7.2	72.9	18.2
	52	<i>S. cinerea</i> ab., no marked domina- ant in ground flora	676.6	12.4	54.5	40
	53		523	16	32.6	67
	84		Saturated		34.0	60.1
	85		"		43.0	51.2

Series IV

41	Closed Carr at Out Dubs (No. 42 near reeds)	375.1	7.8	47.9	36
42		490.7	10.7	45.6	46.3
43		366.1	8.5	42.9	45.4
44		378.8	8.5	43.3	52.3

Series V

86	Closed Carr at North Fen (Nos. 82 and 83 in West of carr)	858	11.0	78	11.3
87		800	11.9	67	24.2
51		1092	15.6	70	22
54		876.5	14.3	62	28.5
82		580.8	12.1	48	42.7
83		516.0	11.8	43.9	38.8

Series VI

	Number of sample	Water Content	Coefficient of Soil Humidity	Humus Content	Ash Content
Reedswamp.	8	—	—	55.9	34.2
	9	—	—	47.8	42.9
Area of rapid silting	95	—	—	52.8	38.5
	96	—	—	54.5	41.4
Silting moderate	88	—	—	53.7	38.2
	89	—	—	56	34.2
	90	—	—	57	35.8
Silting rela- tively slow	91	—	—	57.3	34.7
	92	—	—	58.0	35.0
	93	—	—	60.1	32.0
	94	—	—	61.1	32.6

Series VII

<i>Molinia</i> consocieties succeeding reedswamp	75	593	8.9	66.9	25.1
	76	609	9.6	63.8	29
	77	700	10.5	66.2	23.8
	78	900	13.5	66.2	23.9
	79	1063	15.0	70.4	19.1
	80	770	12.0	64.2	27.8
	47	991	13.0	76	13.1
	48	668.2	11.8	56.3	37.3
	49	964.5	13.5	71	18.4
	50	893	11.2	79.6	12.3

Series VIII

<i>Molinia</i> consocieties succeeding carr	4	518	6	85.4	5.5
	5	777	8.9	86.8	5.1
	6	489	5.8	83.6	6.5
	20	541	6.4	84	7.3
	21	614	7.4	82.5	7.76
	22	628	7.3	86.4	4.5

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ON THE CLASSIFICATION OF AQUATIC PLANT COMMUNITIES

By W. H. PEARSALL

It is probably generally recognised that the classification of aquatic, and to a less degree of marsh, plant communities, is at present in a most confused condition, due partly to our ignorance of the factors controlling them, and partly to the variability and number of the conditions which affect aquatic vegetation. Many of the latter are, indeed, still under debate, and until they have been decided, any classification must remain, in parts at least, provisional.

TYPES OF CLASSIFICATION

At present, three chief methods of classification have been put forward.

(a) Warming (**24**, p. 180) classifies aquatic plants in accordance with their *growth form*. He distinguishes, among others, such vegetative types as the Elodioid (e.g., *Elodea canadensis*, *Potamogeton pusillus*), the Rosette (e.g., *Isoetes lacustris*, *Littorella lacustris*), and the Nymphaea (e.g., *Castalia alba*, *Nymphaea lutea*) types. The recognition this classification gives to the importance of life form is of great value, but at the same time it fails to take into account the wide range of habitats in which different members of the same growth form may be found.

(b) In *Types of British Vegetation* (**21**, p. 188) emphasis is laid on the importance of the *habitat* factor—to the partial exclusion of the life form—as a basis of classification. The sub-formation of waters relatively poor in mineral salts is provisionally distinguished from that of waters relatively rich in mineral salts. It is by no means certain, however, that variation in the amount of dissolved salts is the chief factor controlling aquatic vegetation. This point may be left for further discussion.

(c) Lastly, in the account of the Norfolk Broads contributed by Miss Marietta Pallis to the same work (**12**, p. 214), where the relation between successive plant communities is described—the method of regarding aquatic and fen communities as part of one succession has been applied to British vegetation. A similar method has been adopted by Matthews (**9**) for the vegetation of a small Scottish loch, which affords good examples of biotic succession. In both these cases the developmental point of view is emphasised as a basis of classification, and the successional nature of floating-leaved, reedswamp, and

fen communities is clearly recognised. An examination of the vegetation of the English Lakes¹ confirms the validity of this view, and also shews that the *submerged* communities occur in definite successions, controlled chiefly by the rate at which inorganic silt is deposited. The fen and marsh communities round these lakes succeed the aquatic vegetation, and depend in a similar manner upon the rate of sedimentation. As the peat underlying these communities is raised above the flood level, silting ceases, and "acid" peat is developed, dominated by moor vegetation. *Thus, starting from bare stones and finishing in moor, we have typically one long succession, in the varied development of which, the rate of sedimentation is the principal factor.*

The abundance of moors of lacustrine and estuarine origin in and around the English Lake District, shows that this succession is here the rule rather than the exception. In the case of the larger lakes, however, a more primitive condition is retained on account of their size and depth. While the absence of similar lakes in other parts of England makes it less easy to apply this generalisation to all British lake vegetation, yet the Cheshire meres, the Somerset region (Moss, 10), the Norfolk Fens and Broads (21), seem all to fall in with such a general classification. The Scottish lakes certainly agree with it. The Welsh lakes have not yet been investigated ecologically. The most notable difference in the Fens is, that local conditions (low rainfall and rich soil waters) extend the importance of the *carr* stage, while cultivation, drainage and especially climate limit the development of moor. In this case, also, calcareous waters are, in a certain degree, equivalent in effect to abundant silt.

Since there is one master factor running throughout the development of the above succession, any attempt to divide it must clearly be of an arbitrary nature. Though Moss (11, p. 37) makes such an attempt, he recognises the difficulty of deciding at what point a *habitat* division should be made. A distinction is usually drawn (9, 11, 12) between *aquatic* and *fen* formations—reed-swamps being included in the former. From actual observation, I have concluded that no such line of demarcation is possible. Not only does reed-swamp dominate large areas of land (e.g., Woodwalton Fen in Huntingdonshire), but the type of reedswamp bears a definite relation to the type of fen or marsh succeeding it, both in habitat and floristic (e.g., Esthwaite). The reedswamp must, in short, be regarded both as the *climax aquatic community*, and as the *pioneer fen community*.

In the parallel case of the transition of fen to moor, the *Molinia caerulea* community occupies an exactly similar position. While the life form of the dominant plant is apparently adapted to a *fen* condition—gentle silting—(19), the subordinate members of the community are heathy, and the occurrence of *Molinia* "grass moors," with similar floristic composition, points rather to the inclusion of this community in the *moor* stage of the

¹ For a detailed account of one of these lakes, the reader is referred to the writer's paper on Esthwaite Water in this JOURNAL, 5, p. 180 and 6, p. 53.

succession. There is, moreover, no clear habitat factor indicating the position of the *Molinia* community. While the presence of silting (altogether lacking in moors), should include it among fens, its type of undecayed peat, with low ash content, indicates undoubtedly a close approach to the edaphic conditions of moor¹. Here again, therefore, we cannot distinguish a clear line of division.

The aquatic, fen, and moor successions should therefore be regarded as together forming a unit, for the following reasons: (1) There is a single biotic succession. (2) There is a single controlling physical factor—silt or soil waters rich in bases. (3) There are no outstanding habitat variations subdividing the succession. Though the so-called aquatic, fen, and moor formations (9, 11, 12) have hence little right to be considered as separate entities, they constitute well marked *phases* of the unit as a whole.

NOMENCLATURE

The recent publication of Prof. Clements' *Plant Succession* (1916), has given us a comprehensive terminology, likely to prove of considerable value in classifying such successional plant communities as are dealt with in this paper. In this volume, a complete succession is divided into two types of communities, the *climax* units and the *seral* or developmental units, the latter being distinguished by distinctive name-forms. Thus an *association* is considered as the *climax* equivalent of the *seral associates*. In this way, the nomenclature is designed to indicate whether or not, a community is developmental.

Now the aquatic, fen, and moor succession may most conveniently be regarded as leading up to one *formation*—moor—uniform with those described by Clements, and lending itself admirably to his nomenclature of plant communities. In agreement with Clements' views, this moor formation is apparently primarily conditioned by *climate*, since it is independent of the strata, calcareous or siliceous, underlying it. The causes of its initiation, are both *topographic* and *biotic*, and this also agrees with Clements' conception. There is, however, one difference, due to the fact that these moors are essentially *valley* formations, and not therefore, entirely climatic. With this variation, I propose to adopt Clements' conception of the formation, for the aquatic and fen succession leading up to moor. All the aquatic and fen communities thus become seral units, since they belong to the developmental stages of the formation. For more detailed proof of the seral nature of the communities mentioned below, the reader is referred to the paper on Esthwaite Water (13).

I propose now to take further examples indicating the value and application of Clements' nomenclature, but altering his arrangement of aquatic

¹ All the Lake District fens—while often bearing a close floristic resemblance to those of East Anglia—have *acid* soil waters. Acidity of soil is not, therefore, a distinction between fen and moor.

communities. In the hydrarch succession, he distinguishes (2, p. 137) "three well marked associates, namely, *submerged* plants, *floating* plants and *swamp* plants." This classification agrees essentially with that of Miss Pallis (12), of *submerged leaf*, *floating leaf*, and open and closed *reedswamp* "associations." Miss Pallis, however, remarks on the probability that these are, in reality, groups of "associations," and from my observations, this seems actually to be the case. Taking reedswamp first, as an example we can contrast the community of *Typha latifolia*, characterised by the rapid deposition of inorganic silt, with the community of *Carex inflata* in habitats where inorganic silt is quite or nearly absent. These are seral communities of definite floristic and habitat, each having one dominant; each therefore ranks as a *consocieties* (agreeing with Matthews, 9). The more typical reedswamp of *Phragmites communis* and *Scirpus lacustris*—the latter toward the open water—occupies an intermediate position between these two, and, having two dominants, ranks as an *associates*, in which each of the two zones is a *consocieties*. Thus the reedswamp growth form includes a series of consocieties, much as a climax forest formation may include a group of consociations (see Clements, *loc. cit.*).

A further illustration may be found among floating leaved plants, where the growth form also includes several seral communities. We can here distinguish, as one example, the *Castalia* (*Nymphaea*) *alba* consocieties of moderately rapid sedimentation, from the *Castalia* (*Nymphaea*) *minor* consocieties of very slight inorganic sedimentation.

Lastly, we find that submerged plants include several growth-forms, and also occur on a great variety of habitats, in characteristic communities. Taking the Elodioid first, my observations on the English Lakes shew that three main types of habitat communities exist within this life-type. These are classified in the following summary, and it will be also noticed that these habitat variations coincide with minor variations in life form. All are communities covering large areas, not small or scattered clumps.

1. *The linear leaved associates* is characteristic of relatively rapid inorganic silting, and includes consocieties dominated by one of the following: *Najas flexilis*, *Callitriche autumnalis*, *Potamogeton pusillus*, or *Scirpus fluitans* (deep water form).

2. *The associates of Potamogeton of P. praelongus type* is apparently typical of rather rapid silting. Consocieties are dominated by *P. praelongus*, *P. lucens*, *P. Zizii* (deep water form) or *P. perfoliatus*. (This does not compete with 1.)

3. *The Nitella associates* occurs where silting is moderate, and often succeeds 1 and 2, as the habitat gets more organic. It includes the following consocieties, usually in different lakes: consocieties of *Nitella opaca* or *Nitella flexilis* or *Chara fragilis*¹.

In each of these associates, there are a number of consocieties which approach

¹ Warming (24) includes *Characeae* in the Rosette life form!

one another in ecological equivalence. It is probable that the *invasional* factor may partly determine which consociates dominates a particular water, for the migration of submerged water plants from lake to lake, must be fortuitous to some degree. If, however, two or more equivalent consociates occur in one lake they fuse, and reflect the associates in miniature.

Secondly, the Rosette type of submerged plants is as a whole characteristic of silt-free localities. Nevertheless, there are distinct habitat communities within the growth-form, and these communities are in no way equivalent. We can, in illustration, distinguish: (i) The *Isoetes lacustris* consociates of deep water and no silt, from (ii) the *Littorella-Lobelia* associates of shallow, coarse, unstable habitats. The former passes into the *Nitella* associates if silt accumulates, the latter into floating leaved or reedswamp communities.

Now in the larger lakes the slowness of silting coupled with the depth of the water often make it impossible for the *Isoetes* consociates and the *Nitella* associates to go through the normal seral development, and hence one community is kept on for a long period without changing, the succession being thus fixed in a subclimax stage. In this condition the above communities rank respectively as the *Isoetes* consociation and the *Nitella* association. It would thus seem that Clements' division of the water seres into submerged, floating, and swamp associates fails to take account of the wide habitat variations existing within the range of these major growth forms. Since varying communities included in these life forms exist under different conditions and are severally arranged, they are fully entitled to the higher rank I give them.

Other communities occur, however, which lack the characters distinguishing the above associates and consociates.

In Derwentwater, for example, the typical reedswamps are open, with *Phragmites communis*, *Scirpus lacustris*, and *Equisetum limosum* almost equally abundant. Developed at first on a thick *Littorella-Lobelia* carpet, they may also include *Potamogeton natans*, *P. Zizii*, *P. perfoliatus*, *Castalia minor*, *Nymphaea intermedia*, *Myriophyllum spicatum* and *Juncus fluitans*. At any one place from three to six species of differing life form may be equally abundant. Such a community is a mixture of differing stages of a succession; and these stages happen to be approximately equivalent under the conditions in which these open reedswamps are found. Probably the open reedswamps of the Broads (12) are of a similar nature. Such a mixed community may be called a *mixtum*, in the sense suggested by Tansley (22, footnote, p. 199), and defined as "a transitional mixture of successive seral dominants."

In moderately shallow waters, e.g. the Broads (12), small clumps of *Scirpus lacustris* may appear far in advance of the open or closed community in which this plant normally occurs. Among unrelated life-forms, and bearing no fixed relation to the habitat, these clumps can only be regarded as detached initial stages of a later seral dominant. Such small groups of one species, characteristic of bare areas and initial stages, Clements terms *families*.

Littorella lacustris also forms families on exposed, unstable gravel, long in advance of the *Littorella-Lobelia* associates. *Sparganium natans* almost confines itself to this type of vegetative unit. It grows on bare stones, or on mud where other factors (e.g., very turbid water) inhibit the development of submerged vegetation, and then shews nothing in common with other floating-leaved communities, except a need for shelter.

HABITAT FACTORS

After these brief indications of the value and application of Clements' nomenclature, we may pass on to consider the habitat factors governing the earlier stages of water seres. This phase of the subject involves the discussion of two questions: (1) What constitute habitat differences among water plants? (2) How are aquatic plants related to these differences?

The provisional distinction of "waters poor in mineral salts" from those "rich in mineral salts" was an attempt to answer the first of these two questions. But though this distinction coincides with Graebner's classification (7) of the fundamental habitat factors, it does not appear to be truly applicable to all aquatic vegetation.

A water, poor in mineral salts, may yet, especially in flood, bring down vast quantities of sediment. While this sediment may have no effect upon the mineral residue of the water, it may, even if chemically inert, have an enormous effect upon the aquatic communities, primarily because of its intimate relation with the physical nature of the substratum. This condition is very well marked at Esthwaite, especially in contrast with larger lakes, and adjacent upland tarns. Still more important in this country is the fact that waters rich in mineral salts lie in areas geologically stable, and overlaid by finely divided superficial layers, easily transported by water. Such waters will contain, in flood, if not normally, a large proportion of suspended matter. In consequence, lakes, pools, and broads tend to be silted up, and as a result, few of these richer waters shew primitive features (e.g., irregular or coarse substrata). Particularly is this the case in calcareous areas.

The distribution of waters poor in mineral salts corresponds, on the whole, with that of mountainous regions and hard rocks, where the majority of the lakes are in a comparatively primitive condition. As a result, the marginal slopes of such lakes are often steep, and their composition is normally coarse. These regions are also characterised by relatively great surface change, and therefore they shew many unstable habitats. Thus the plant communities of waters poor in mineral salts are developed under a series of conditions which usually occur together in this country, but are not necessarily related. They may be summarised as follows: (i) Waters poor in mineral salts, (ii) Waters usually rather poor in inorganic silt, (iii) Substrata either (a) coarse and primitive, (b) under erosion and unstable, or (c) only slightly and recently sedimented.

Such substrata may support plants of widely diverse types, not necessarily depending primarily on the paucity of salts in the water. Prominent among them will be plants with a *colonising* rôle. There will be also plants of *inorganic* silts, and perhaps true *silicicole* plants. On the other hand, as the absence of inorganic bases prevents the decay of humus, we shall also find plants of *undecayed peat*, a condition akin to that of terrestrial moors.

There is obviously, therefore, a danger of confusing plants characteristic of waters poor in mineral salts, with those found colonising the products of recent erosion, or sedimentation. In old, silted up waters the silting factor becomes of little importance; and since the colonising stages are quickly passed over, colonising plants are less typical. The paucity of species in many primitive lakes is certainly due primarily to the absence of sediments (i.e., suitable substrata), rather than to the paucity of their waters in mineral salts.

The *Littorella lucustris* community is one of the most characteristic of the colonising stages, and it typically develops on barely stable gravel. West (25) records it in Lindores and Lochmill Lochs, and also as forming bottom carpets in Carlingwark Loch. All these are calcareous waters. He observes further that it is less abundant in the calcareous Lismore area than in the Loch Ness region. His list of species indicates, however, an advanced state of sedimentation in the Lismore lakes, and therefore, few coarse substrata. Crampton (3) also records this plant in calcareous waters in Caithness. Thus the *Littorella* community does not appear to be conditioned primarily by waters poor in mineral salts.

Sparganium natans is a similar colonising plant. It occurs in two calcareous waters in the Furness district—Urswick Tarn and a pool by the railway near Barrow. In each case the water has a dissolved mineral residue of over .2 gm. per litre, but has no submerged plants, their absence being due to the extreme turbidity of the water. The consequent lack of competition on abundant silt, is accompanied by the growth of this colonising plant, usually confined to waters poor in mineral salts. The *Najas flexilis* consociates of Esthwaite Water also appears to be a colonising community, but a study of its habitat elsewhere is needed, before we can accept this definitely.

The chief habitat factors governing the distribution of aquatic vegetation in lakes seem to be: (i) Large variations in the dissolved mineral and organic contents of the water, (ii) Variations in the amount and type of sediments deposited and the effect of these on the substratum, (iii) The physical and chemical nature of the primitive lake floor—if exposed.

There is probably a certain degree of equivalence between dissolved and suspended matters. There are probably also *calcicole* and *calcifuge* aquatic plants, and we may, in addition, expect aquatic plants to shew affinities with regional floristic variations¹. On the other hand, just as there are

¹ Cf. Magnin (8).

terrestrial plant communities of organic and inorganic soils, there are also aquatic communities of these habitat types. In the same manner as we can distinguish terrestrial organic soils according as their rate of decay is rapid (e.g. *fens*), or slow (e.g. *moors*), so we can distinguish sub-aquatic soils of these types, with their corresponding floristic variations.

The future classification of aquatic plant communities may perhaps proceed, therefore, on lines closely analogous to those of terrestrial communities, and the conditions indicated above should control the starting points. In view of the great number of variations possible in these conditions, emphasis laid on the successional nature of the communities would seem to give the only unified method of treatment possible. Especially would unity be achieved if the final development of moor from water seres were found to be general throughout the British Isles, which I believe to be probable.

We will now turn to the second question raised in this section, viz. how are aquatic plants related to the substratum? Three prevalent views bearing directly on this point must be considered. It is stated by some authors that aquatic plants have roots which lack root-hairs, and whose only function is fixative. Others declare these plants to be normal in this respect. Brown (1) suggests that the relation of *Elodea* (and probably other plants) to organic soils is possibly due to the local concentrations of carbon dioxide over such substrata. He found that free floating *Elodea* was apparently independent of the substratum, if supplied with abundance of carbon dioxide. It is doubtful however, how far such experiments can be related to the conditions of plant life in lakes. From Delebecque's (5) experiments on the French lakes where 38–40 c.c. of carbon dioxide per litre were present, at temperatures ranging from 4.5° to 20.5° C., and from a few personal observations on English lakes, which agree remarkably with his results, it is found that the normal variation possible is so slight (·2 %), as to be negligible. Brown's assumption is further negated by the fact of the known and continual movements of lake waters, even in sheltered places¹; these would inevitably prevent such assumed local concentrations of dissolved matters. Thus we are driven to conclude that aquatic plants are related to their substrata through their roots.

Schenk (18), Sachs (17), Vines (23), and Warming (24) consider that aquatic plants absorb nutrient salts throughout their entire surface, their roots being purely fixative, but they do not support their contention by experimental evidence. Pfeffer (14), after reviewing the literature in 1897, concluded that no decisive experiments had been made to confirm either view. Since then (1905), Snell (20) and Pond (16) found independently, that *Elodea canadensis*, *Myriophyllum spicatum*, *Potamogeton obtusifolius*, *P. perfoliatus*, *Ranunculus trichophyllus* and *Vallisneria spiralis* grew more vigorously when rooted in the substratum than when anchored over it, and

¹ Gilbert (6), and numerous authors in *Proc. Roy. Soc. Edin.*

especially when rooted in *soil* not *sand*. Hence they concluded that the roots have an absorptive as well as a fixative function.

The known differences in aquatic plant communities on different substrata¹ agree with this conclusion. These differences are especially marked in the English Lakes.

Further it seems highly probable that most aquatic plants develop root hairs. I have observed these structures in the following species: *Najas flexilis*, *Hydrilla verticillata*, *Elodea canadensis*, *Scirpus fluitans*, *Potamogeton pusillus* (agg.), *P. obtusifolius*, *P. praelongus*, *P. lucens*, *P. perfoliatus*, *P. heterophyllus*, *P. Zizii*, while Pond (16) also records them in *Potamogeton pectinatus*, *P. pauciflorus*, *P. natans*, *P. zosterifolius*, *Ranunculus trichophyllus*, *Vallisneria spiralis*.

This necessarily brief review of the evidence points toward the conclusion that aquatic plants bear a relation to the substratum not markedly dissimilar from that of terrestrial plants, in absorbing nutrient salts through their roots. If this indeed be the case, there is all the less reason for considering aquatic communities as a separate ecological unit, and we may further conclude that their correlation with terrestrial communities into one succession, is as justifiable in this sense, as it is from the point of view of development.

Finally, I may point out that the system of classification adopted here coordinates, to a great extent, the conceptions underlying the previous classifications here reviewed. While the basis of the vegetational unit is the development of a biotic succession, growth form and habitat become factors of fundamental importance in considering the distribution of individual component communities, and in determining their status. The difficulty of deciding which of these two factors is the more important in assigning formational rank to types of vegetation, is thus avoided. The further difficulty of securing agreement as to what constitutes fundamental identity of habitat does not apply to the unit of vegetation here defined. Moreover, this unit is exceedingly flexible, since it allows the inclusion of the most diverse starting points in the successions composing it.

I must, in conclusion, express my indebtedness to Mr A. G. Tansley, for his valuable suggestions on nomenclature.

¹ Pieters (15), Brown (1).

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THE BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING

The Eleventh General Meeting (the Fourth Annual General Meeting) was held on Dec. 15th, 1917, in the Botanical Theatre, University College, London, at 10.30 a.m. The Chair was taken by Prof. F. W. Oliver. The minutes of the last Annual Meeting and of the Field Meeting at Rothamsted were read and confirmed and the Hon. Secretary then presented his Report for the past year.

HON. SECRETARY'S REPORT FOR 1917

During the past year the activities of the society have necessarily been of a somewhat restricted character. Two meetings, as required by our constitution, have been held, namely, the Annual General Meeting in London, and a field meeting at Rothamsted. A third meeting was contemplated in connection with the British Association at Bournemouth, but was necessarily involved in the abandonment of that fixture. In this connection criticisms have been received from one or two members in which complaint is made that most of our meetings recently have been held in the South of England. The Hon. Secretary is therefore glad of this opportunity of repudiating the suggestion that the Council is intentionally favouring a particular section of the members. In 1916, owing to war conditions, only one Meeting, the Annual General Meeting, was held. We have thus had three meetings during the past two years of which two must, by our Rules, be held in London. The meeting at Rothamsted last summer was first suggested to the Council by one of our North-of-England members and had been contemplated for some time. Most of our members are probably aware that it is not easy at the present time to ensure good attendances at meetings, and London is the only centre at which a large proportion of the membership is able to be present. The high railway fares make it impossible to rely on the presence at meetings, of members from a distance. But though the distribution of the membership would warrant a preponderance of meetings in the south it is the policy and intention of the Council that in normal times meetings should be held equally in the North as in the South, irrespective of the localisation of the majority of the membership.

It was naturally anticipated that, with the many and unlooked for demands entailed by the war, there would be an appreciable diminution in our numbers. But it is satisfactory to be able to announce, that only five resignations have been received during the past year, though in addition we have to deplore the loss of two members by death, Dr S. M. Baker, who was only elected to the council last year, and Lieut. D. Macpherson who died of wounds on the 11th of November. Mr Macpherson's death adds one more to the serious losses which we, in common with Science generally, have sustained through the war, leaving gaps that cannot well be filled. On the other hand seven new members have been added during the past twelve months. Our total membership thus stands at 111, the same number as in 1916.

There is one other matter to which, as the officer of the Society primarily responsible to the members, the Hon. Secretary would like to refer. Several inquiries have reached him regarding the Society's Library, the use of which is enumerated amongst the members' privileges. It had been hoped at the outset to organise a library the nucleus for which would be provided by books received for review, etc. A certain number of books and papers have accumulated in this way but not to the extent that was anticipated. Moreover the difficulties of housing and organising a library under present conditions and of rendering it available to members, are such that for the present it has been decided to delete this from the list of facilities which the Society affords.

Finally the Hon. Secretary wishes to appeal to the members in general to be more prompt in the payment of their subscriptions. It is fully realised that this delay is largely the result of the many demands on time which make even the writing of a cheque seem irksome. Probably however it is not realised that this neglect involves an even greater sacrifice of time on the part of the Society's officials, time which they can as ill afford as the private member, and entails additional expenditure at a time when the greatest economy is essential.

The Hon. Treasurer in presenting the Accounts for 1916 (see p. 87), which were unanimously adopted, pointed out that the adverse balance had been completely wiped out and all liabilities met. The year 1917 promised to turn out as favourable as 1916. On the proposal of Mr Watt the thanks of the Society were accorded to Mr Chas. Oldham, who had kindly audited the accounts.

The following alterations of the Rules, of which due notice had been circulated to members, were passed by a majority of more than two-thirds of those voting.

That Rule 9 shall read:

The Society is governed by a Council of 14 members, including the President, two Vice-Presidents, the Hon. Editor, the Hon. Secretary and the Hon. Treasurer of the Society.

That Rule 11 shall read:

The Officers of the Society are the President, two Vice-Presidents, the Hon. Editor, the Hon. Secretary and the Hon. Treasurer. The President and two Vice-Presidents shall be nominated from among existing members of the Council. The Hon. Editor and Hon. Secretary retire at the end of each year, but are eligible for re-election.

That Rule 16 shall read:

The Hon. Secretary is an Officer elected at the General Meeting and is a member of the Council. He acts as Secretary and is responsible for the collection of subscriptions.

That the following rules be added:

16 A. The Hon. Editor is *ex officio* a member of the Council.

16 B. If any Council member does not attend at least one meeting of the Council during the year he shall retire at the end of that year, but is eligible for re-election.

The abrogation of Rule 11 for the present Meeting was agreed to and the Council's nominees were duly elected as follows:

President, Dr W. G. Smith; *Vice-President*, Prof. R. H. Yapp; *Hon. Editor*, Mr A. G. Tansley; *Hon. Secretary*, Dr E. J. Salisbury; *Council Members*, Messrs C. A. Cheetham, R. Paulson, G. Morris.

The formal business having been concluded Mr Tansley communicated "Notes on Succession," in which he laid stress on the fact that by no means all the successions actually recorded are organic unities, as Clements postulates. In some cases a number of phases of succession are characterised by a progressive change in the vegetation determined by a definite group of related ecological factors, but in others the successive phases are determined by incidental factors not so related. These two classes of cases must be clearly distinguished. To the second class the conception of the formation as an organism with a definite development does not apply. Prof. Oliver, Mr Wilmott, Mr Fagg, Dr Salisbury and Dr Rayner took part in the discussion.

Mr R. Paulson dealt with "The Ecology of Lichens as illustrated by Woodland and Heath around London." The author called attention to the greater prevalence of corticolous lichens in those parts of the woods situated on clayey soils as compared with those where the soil was sandy. In general too the corticolous lichen flora was much more abundant on the southern sides of the trunks than on the northern. No indication of height zones was observed.

INCOME AND EXPENDITURE FOR THE YEAR 1916.

<i>Income</i>		<i>Expenditure</i>	
	£ s. d.		£ s. d.
Subscriptions received ...	73 10 0	<i>Journal of Ecology</i> —Cost for 1916 ...	188 2 3
Subscriptions to receive ...	32 11 0	Secretary and Editor—Honorarium ...	25 0 0
	106 1 0	Postages and Sundries—Secretary ...	2 10 1
Written off ...	2 2 0	Balance—Surplus on the year, carried to Balance Sheet below ...	51 13 9
British Vegetation Committee. Share of profits on sales of <i>Types of British Vegetation</i> ...			
<i>Journal of Ecology</i> —Sales ...	18 18 9		
	144 8 4		
	<u>267 6 1</u>		<u>267 6 1</u>

BALANCE SHEET AT 31st DECEMBER, 1916.

<i>Liabilities</i>		<i>Assets</i>	
	£ s. d.		£ s. d.
<i>Journal of Ecology</i> —Balance due to Publishers and Editor ...	43 13 11	Cash at London, County and Westminster Bank ...	41 12 3
Sundry Creditors ...	28 7 7	Subscriptions to receive ...	32 11 0
	<u>72 1 6</u>		
Balance—Deficiency brought forward from 31st Dec., 1915 ...	49 12 0		
Surplus on year 1916, as above ...	51 13 9		
	<u>2 1 9</u>		
	<u>74 3 3</u>		<u>74 3 3</u>

HUGH BOYD WATT,
Hon. Treasurer.

I have examined the accounts for the year ended Dec. 31st, 1916, and certify them to be a correct statement and that all vouchers are in accordance with receipts and payments shown therein.

CHAS. OLDHAM.

October 25th, 1917.

The Meeting then adjourned for lunch in the College Refectory after which the points raised by Mr Paulson were discussed.

Prof. Oliver described a method of demonstrating accretion on sandy and muddy foreshores by means of a layer of coloured sand, obtained from Alum Bay, sifted on to the surface of the soil. Specimens were exhibited to illustrate the effectiveness of the method. As examples of the results obtained the author stated that accretion was most rapid under *Fucus humicola* and *Pelvetia canaliculata*, where a rise of 3 ins. was observed in 2 years 5 months. In the same period a rise of $2\frac{1}{2}$ ins. was found in dense *Salicornia* whilst high saltings shewed only 0.4 in.

Dr Salisbury next communicated an account of the British *Quercus sessiliflora* woods. The view was advanced that whilst shallowness of soil undoubtedly explained the dominance of this species in certain cases it failed to explain its presence in others. All the woods of this type however appeared to agree, except where growing on calcareous soils, in being associated with a low proportion of mineral salts in the soil solution as compared with that of *Quercus robur* woods. The occurrence on calcareous soils was probably to be explained as due in some cases to the shallow character of the soil, in others to the high rainfall and consequent dilution and leaching of the mineral salts from the surface layers. The various societies present in these woods were described and their probable relationship to light-intensity, water-content and acidity pointed out.

A discussion followed in which many of those present took part.

A paper on "Succession on the Liassic cliffs of the Glamorgan Coast" was then read by the author, Miss Golding (introduced by Prof. Trow), in which the phases from grassland to scrub and wood were described and also those resulting from erosion. The pioneer plants were found to be phanerogams and not cryptogams as might have been expected.

By the kind hospitality of Prof. Oliver the members were subsequently entertained to tea in the Botanical Department.

E. J. SALISBURY,
Hon. Sec.

LIST OF MEMBERS (JANUARY 1ST, 1917)

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, Dr E. J. SALISBURY, The Briars, Crosspath, Radlett, Herts.

Accessions Dept. Library, Columbia University, New York.

Adamson, R. S., M.A.; Botanical Dept., University, Manchester.

Aimer, James; Technical School, Bell Street, Dundee.

Andersonian Naturalists' Society (*Secretary*, H. G. Cumming, 90, Barrington Drive, Glasgow).

Armitage, Miss E.; Dadnor, Ross, Herefordshire.

Bews, Prof. J. W.; University College, Pietermaritzburg, Natal, S. Africa.

Birt, Miss E.; 22, Denmark Terrace, Brighton.

Blackman, Prof. V. H., F.R.S.; Imperial College of Science, London, S.W.

Blackwell, Miss E. M., M.Sc.; 16, Stanley Avenue, Birkdale, Southport.

Blatter, Father E.; St Xavier's College, Bombay.

Bolland, B. G. C.; Department of Agriculture, Cairo, Egypt.

Bournemouth Natural History Society (*The Librarian*, Municipal College, Lansdown, Bournemouth).

Brenchley, Dr Winifred E.; Rothamsted Experiment Station, Harpenden, Herts.

Brennan, A.; Technical College, Newport, Mon.

Brooks, F. T., M.A.; Botany School, Cambridge.

- Brown**, George, M.A.; School House, Littlemill, Patna, Ayrshire.
- Brumfield**, Dr D. M.; State University, Iowa City, Iowa, U.S.A.
- Bureau of Science** (Librarian), Manila, Philippine Islands.
- Carter**, H. G., M.B.; Royal Botanic Gardens, Calcutta.
- Cavers**, Dr F.; 190, Addison Way, Golders Green, London, N.W., *Hon. Life Member*.
- Cockayne**, Dr L., F.R.S.; Ngaio, Wellington, New Zealand.
- Cotton**, A. D.; Herbarium, Royal Gardens, Kew.
- Croydon Natural History and Scientific Society** (Miss Grace Bigby, 15, Stonehill Mansions, Streatham Hill).
- Crump**, W. B., M.A.; 4, Marlborough Avenue, Halifax, Yorks.
- Cutting**, E. M., M.A., B.Sc.; 125, Tredegar Street, Bow, London, E.
- Darbishire**, Dr Otto V.; Botanical Dept., University, Bristol.
- de Fraine**, Dr Ethel; 27, Bargery Road, Catford, London, S.E.
- Delf**, Dr E. M.; Westfield College, Hampstead, London, N.W.
- Dewar**, Dr J. M.; 5, Chalmers Street, Edinburgh.
- Drabble**, Dr Eric; 13, Claverley Grove, Church End, Finchley, London, N.
- Essex Field Club, The** (Essex Museum of Natural History, Romford Road, Stratford, Essex).
- Farmer**, Prof. J. B., F.R.S.; Imperial College of Science, London, S.W.
- Farrow**, Dr E. P.; Limehurst, Spalding, Lines.
- Fritsch**, Prof. F. E.; 77, Chatsworth Road, Brondesbury, London, N.W.
- Gordon**, G. P., B.Sc.; West of Scotland Agricultural College, Blythswood Square, Glasgow.
- Halket**, Miss A. C., B.Sc.; Bedford College, Regent's Park, London.
- Hampstead Scientific Society** (*Librarian*, 92, Fellows Road, Hampstead, N.W.).
- Hartshorn**, John; School House, Leyburn S.O., Yorkshire.
- Henkel**, J. S.; Conservator of Forests, Pietermaritzburg, S. Africa.
- Hill**, T. G.; 9, Bloomfield Terrace, Pimlico, London, S.W.
- Howarth**, W. O.; 61, Cecil Park, Crouch End, N. 8.
- Hume**, Miss E. M. M.; 57, Doughty Street, London, W.C. 1.
- Jefferies**, Rev. T. A.; The Manse, Littleborough, near Manchester.
- Jeffreys**, H., M.A., M.Sc.; 199, Albany Street, Regent's Park, N.W. 1.
- Jenkin**, T. J., B.Sc.; University College, Bangor, N. Wales.
- Jewson**, Miss S.; 3, Devonshire Place, Newcastle-on-Tyne.
- Johns**, D., B.Sc.; County Education Office, Carmarthen, S. Wales.
- Johnson**, Miss Edith; 63, Oriel Road, North End, Portsmouth.
- Johnstone**, Miss Mary; 43, Hill Top Avenue, Cheadle Hulme, Cheshire.
- Jones**, Miss G. M.; The Cottage, Wraysbury, Wilts.
- Laurie**, Miss C.; 1, Vittoria Walk, Cheltenham.
- Macgregor**, M.; 33, George Square, Edinburgh.
- Maclean**, Dr R. C.; Duart, Holmes Road, Reading.
- Mangham**, S., M.A.; Armstrong College, Newcastle-on-Tyne.
- Matthews**, J. R., M.A.; Birkbeck College, London, W.C.
- Morey**, F.; Wolverton, Carisbrooke Road, Newport, Isle of Wight.
- Morris**, George, B.Sc.; Friends' School, Saffron Walden, Essex.
- Moss**, Dr C. E.; Technical College, Johannesburg, Transvaal.
- Negri**, Dr Giovanni; R. Istituto Botanico, Torino, Italy.
- Newman**, Leslie F., M.A.; School of Agriculture, Cambridge.
- Nicholson**, C.; 35, The Avenue, Hale End, Chingford, E. 4.
- Oakley**, W. J.; 20, Head Street, Halstead, Essex.
- Oldham**, Charles; The Bollin, Shrublands Road, Berkhamsted, Herts.

- Oliver**, Prof. F. W., F.R.S.; University College, London, W.C.
Oliver, W. R. B.; 5th Avenue, Tauranga, New Zealand.
Orr, M. Y.; Royal Botanic Gardens, Edinburgh.
Osborn, Prof. A. H.; University of Adelaide, Australia.
Pallis, Miss Marietta; Aigburth Drive, Liverpool.
Paulson, R.; Glenroy, Cecil Park, Pinner, Middlesex.
Pearsall, W. H., M.Sc.; Ivy Dene, Dalton in Furness, Cumberland.
Pearse, Miss Eleanor; 3, Bessborough Mansions, Vauxhall Bridge Road, S.W.
Pearson, A. A.; Goodacre, 81, George's Avenue, Weybridge.
Porter, Mrs. B.Sc.; 3, Brighton Villas, Cork, Ireland.
Praeger, R. Lloyd; National Library, Kildare Street, Dublin.
Price, S. R., M.A.; Botany School, Cambridge.
Quick, B. E.; Lowell, Michigan, U.S.A.
Radley, L. W.; 8, Croxted Road, Dulwich, London, S.E. 21.
Ramsbottom, J., M.A.; Botanical Dept., Natural History Museum, London, S.W.
Randell, Miss F. A.; 37, Temple Street, Oxford.
Rayner, Dr M. C.; University College, Reading.
Rübel, Dr E.; Zürichbergstrasse 30, Zürich, Switzerland.
Salisbury, Dr E. J.; The Briars, Crosspath, Radlett, Herts., *Hon. Secretary*.
Shelford, Prof. Victor E.; 506, W. Iowa Street, Urbana, Illinois, U.S.A.
Skene, Macgregor, B.Sc.; Avondow, Milltimber, Aberdeen.
Smith, Dr William G.; 9, Braidburn Crescent, Edinburgh, *Hon. Life Member, President*.
Smith, Miss Winifred; A 62, York Terrace, Regent's Park, N.W.
Stapf, Dr O., F.R.S.; Herbarium, Royal Gardens, Kew.
Stapledon, R. G., M.A.; University College, Aberystwyth.
Stevenson, Miss E. H.; 28, Foxcombe Road, Weston, Bath.
Stiles, W., M.A.; 35, Rylett Road, Shepherd's Bush, London, W. 12.
Sutherland, Prof. G. K.; Hartley University College, Southampton.
Tansley, A. G., F.R.S.; Grantchester, Cambridge, *Hon. Editor of the Journal*.
Taylor, Norman; Brooklyn Botanic Garden, Brooklyn, N.Y., U.S.A.
Thoday, D., M.A.; The University, Manchester.
Trow, Prof. A. H., D.Sc.; 50, Clive Place, Penarth, Glamorgan.
Vines, Prof. S. H., F.R.S.; Botanic Garden, Oxford.
Waterfall, C., F.L.S.; Dalmeny, Shavington Road, Chester.
Watson, W., D.Sc.; Taunton School, Taunton, Somerset.
Watt, Hugh Boyd; 77, Parliament Hill, Hampstead, London, N.W. 3, *Hon. Treasurer*.
Weiss, Prof. F. E., F.R.S.; University, Manchester, *Vice-President*.
Wells, Dr Morris M.; Dept. of Zoology, University of Chicago, Chicago, Illinois, U.S.A.
West, George; Burnside, Woodhaven, Wormit, Fife.
Willan, G. R.; Glan-yr-Afon, Cefn Coed, Merthyr Tydfil, S. Wales.
Williams, Miss W.; 68, Trinity Street, Barry.
Williams, Prof. Lloyd; University College, Aberystwyth.
Wills, Miss Lucy; 57, Doughty Street, W.C. 1.
Wilmott, A. J., M.A.; Botanical Dept., Natural History Museum, London, S.W.
Woodhead, Dr T. W.; Technical College, Huddersfield, Yorks.
Woodruffe-Peacock, Rev. E. A.; Cadney Vicarage, Brigg, Lincs.
Wortham, Miss W. H.; The High School, Kendal.
Yapp, Prof. R. H., M.A.; Queen's University, Belfast, Ireland, *Vice-President*.
Yorkshire Naturalists Union (**C. A. Cheetham**; Stonebridge Mills, Wortley, Leeds).

CONSTITUTION AND RULES

I.—OBJECT

1. The object of the British Ecological Society is to promote and foster the study of Ecology in its widest sense.

II.—MEMBERSHIP AND SUBSCRIPTION

2. The Society consists of Members and Associates, as defined in Rules 3 to 8 below.

3. Membership or Associateship is open in the first instance to all on payment of the respective Annual Subscriptions.

4. The Annual Subscription for Membership is One Guinea, payable in advance, and is due on January 1st in each year.

5. Members have the following privileges:

(a) Of receiving the Journal post free.

(b) Of receiving on application any other publications of the Society free or at a reduced rate, so far as the funds of the Society may permit.

(c) Of having the use on loan, under regulations, of photographs or lantern slides in the Society's collection.

(d) Of voting in the election of Council and of Officers.

(e) Of being eligible for election to the Council and Committees, or as Officers.

6. The Annual Subscription for Associateship is Seven Shillings and Sixpence, payable in advance and due on January 1st in each year.

7. Associates are entitled to attend meetings and Excursions, to obtain through the Secretary such advice and assistance as the Society can afford, to have the use of the collection of photographs (see 5 c), but they have not the privileges of members indicated in 5 a, 5 b, 5 d, 5 e.

8. NATURAL HISTORY SOCIETIES may subscribe to the Society not less than One Guinea per annum and are thereby entitled

(a) to one copy of the Journal post free;

(b) to such advice and assistance as the Society can afford;

(c) to send two delegates to the Society's meetings, such delegates to have the same privileges as Associates as regards such meetings.

III.—GOVERNMENT

9. The Society is governed by a Council of 14 Members, including the President, two Vice-Presidents, the Hon. Editor, the Hon. Secretary and the Hon. Treasurer of the Society.

In the first instance the Council shall be the existing Members (12 in number) of the British Vegetation Committee resident within the British Isles.

10. Two members of Council, other than the Officers, retire annually in rotation and are ineligible for re-election until the Annual Meeting of the year following that of their retirement.

IV.—OFFICERS AND DUTIES

11. The Officers of the Society are the President, two Vice-Presidents, the Hon. Treasurer and the Hon. Editor, and the Hon. Secretary. The President and two Vice-Presidents shall be nominated from among existing members of the Council. The Hon. Editor and Hon. Secretary retire at the end of each year, but are eligible for re-election.

12. The President of the Society holds office for two years, and it is his duty to deliver an address to the Society at the Annual Meeting next after that at which he was elected.

13. The President is *ex officio* Chairman at all meetings of the Society and Council.

14. One Vice-President is appointed each year and holds office for two years. In the absence of the President it is the duty of the senior Vice-President or in his absence that of the junior Vice-President to take the Chair at meetings of the Society and of the Council.

15. The Treasurer holds office for three years, but is eligible for re-election.

16. The Hon. Secretary is an Officer elected at the General Meeting and is a member of the Council. He acts as Secretary, and is responsible for the collection of subscriptions.

16 A. The Hon. Editor is *ex officio* a member of the Council.

16 B. If any Council member fails to attend once throughout one year he shall retire at the end of that year, but is eligible for re-election.

V.—ELECTION OF COUNCIL AND OFFICERS

17. The Secretary shall circulate to all Members of the Society, one month before the Annual Meeting, a list of the Members of Council including Officers, indicating those who retire according to the rules (see 10) and adding the names of the nominees of the Council to fill the vacancies.

18. Any Member may ballot at the Annual Meeting for any duly qualified Member in place of one of the Council's nominees.

19. The Council has the power to co-opt any Member of the Society to fill vacancies occurring during the year among the Council or Officers, the tenure of such Member, as a co-opted Member of Council, to terminate at the next Annual Meeting.

VI.—MEETINGS

20. The Annual Meeting of the Society is held in December in London.

21. At least one other meeting is held in the year out of London. Further meetings, including excursions, may be held at such times and places as the Council may from time to time determine.

22. At the Annual Meeting, the Members of the Society present ballot for Officers and Council, and consider any other business brought before them by the Council, or by any Member, of which six weeks' notice has been given to the Secretary.

23. Alterations of the rules may be made at the Annual Meeting alone and require six weeks' notice to the Secretary and a two-thirds majority of the Members voting.

24. Members desiring to present communications at any meeting must give six weeks' notice to the Secretary stating the nature of the communication and the time required. The Secretary will include such communications as have been accepted by the Council on the programme of the meeting, to be circulated to all Members one month before the meeting.

25. The Chairman decides as to procedure and the order of business. It is within the Chairman's discretion to admit communications or any business other than the alteration of rules not included in the programme.

VII.—JOURNAL

26. A quarterly Journal called "The Journal of Ecology" is issued by the Society and is sent post free to all Members.

27. The Subscription price of the Journal to others than Members of the Society is Fifteen Shillings per annum, post free. The price of single issues is Five Shillings net.

IN MEMORIAM

Donald Macpherson

DONALD MACPHERSON was educated at George Heriot's School, Edinburgh, and later matriculated at the University. Amongst other distinctions he obtained the Gold Medal for the best herbarium of the session, and in bringing together this collection he worked not only the Highland Arctic-alpine centres but also well-known English areas, including Bristol and Southport. Descended from an old race of Speyside farmers, Macpherson had a distinct leaning towards Agriculture and graduated B.Sc. in that school. He was awarded in 1912 the Steven Scholarship in Agriculture (£75 for one year), and the following year the Vans Dunlop (£100 for three years). The same year an Agricultural Survey was planned by the Board of Agriculture for Scotland and the Edinburgh and East of Scotland College of Agriculture, with grants from the Development Commission. An essential part of the project was a field observer who would live at centres in the area under survey, and there collect information relative to the natural and economic conditions. Macpherson's combined knowledge of field botany and agriculture, and his appreciation of new problems, were just the qualities requisite, and his selection was amply justified in every respect. The post was one of great responsibility, because the field observer was literally the eyes and ears of the survey. This was begun on an area of sheep-grazing hill country, and one primary problem was the relationship between the natural herbage and the size and quality of flocks. The survey involved the preparation of a series of field-maps (of which about 120 sq. miles were completed on six-inch ordnance maps), the acquiring of information as to the grazing value of the more abundant plants, the possibilities of increasing the better herbage and of reducing the less valuable. Incidentally, areas for a chemical soil survey had to be selected, and samples collected of soils and soil waters. In every respect Macpherson carried out his work thoroughly, and his tact and courtesy were great assets in acquiring information on the economics of the countryside.

Mr Macpherson was known to few members of the B. E. S. His one appearance south, during the survey period, was when he read a paper at the Manchester Meeting of the British Association on "Types of Upland Grazings, their economic value and improvement." Another portion of his work forms the basis of a communication in the present number.

But the claims of the survey had to give place to a greater call, one which Macpherson felt strongly from the beginning of the war. A period with the Edinburgh University O.T.C. was followed by further training in Bucks. and at Oxford, then he obtained a commission in the Scottish Horse. The winter of 1916-17 was spent in Lincolnshire, mainly in training infantry with a success acknowledged by his C.O. Then followed an application and transfer to the R.F.A. with a view to more active service. He went to France early last September, and in his first action, on the Menin road, he was wounded in the back. In hospital at Leith, it seemed as if recovery were a matter of time, but complications ensued and he died November 11th, aged 31 years.

As student, assistant in teaching, and in the field, one saw most aspects of Macpherson, and they were ever pleasant. Best of all were the opportunities of joining him in the field. It was somewhat of a task to keep up with the long striding pace of a very tall companion, but it was a great opportunity to see the vegetation of a complex area resolving itself into a methodical scheme. No distance was too great and no hill too steep if there was need to complete a zone of vegetation or to fill in an unfinished boundary. A wet day was regarded as lost to mapping, but it was utilised in working up notes and discussing observations. The problems of vegetation survey were fully appreciated by Donald Macpherson, and one always felt that he was an assured pioneer in the future development of the primary surveys.

W. G. S.

NOTICE OF PUBLICATION OF GENERAL BEARING

POND SNAILS AND WATER PLANTS

Boycott, A. E. "The habitats of freshwater Mollusca." *Journal of Conchology*, **15**, Jan. 1918.

In his presidential address to the Conchological Society Dr Boycott has not only made a distinct contribution to animal ecology but touches on problems which are of considerable interest to biologists generally. The address is based on observations on the aquatic snails in the Parish of Aldenham in Hertfordshire and mainly concerns a critical examination of 135 ponds. These latter fall into two classes according as they exhibit a flow of water (running ponds) or not (closed ponds). Of the 113 examples of closed ponds 27 contained no snails and of these 5 are permanently muddy ponds and 14 are more or less shaded by trees. There appears to be a close association between the occurrence of snails and plants. "On the average ponds with no snails contain 1.7 sorts of the larger water plants, and both numbers increase together till the figure for ponds with five or more sorts of snails reaches 5.4 sorts of plants." The deficiency of vegetation in the muddy ponds suggests that the effect of illumination upon the molluscan fauna is an indirect one.

The supply of oxygen appears to be an important factor; thus the River Colne yielded 26 species of snails, the running ponds with a continuous flow an average of 7.5 species and the closed ponds an average of only 2.3 species. Perhaps the amount of vegetation is important in this connection as well as in relation to the food supply. The special distribution of the individual species indicates that the results are the outcome of habitat differences rather than of inequalities of dispersion.

The following species were only found in the river: *Planorbis corneus*, *Bithinia tentaculata*, *B. leachii*, *Valvata piscinalis*, *V. cristata* and *Pisidium amnicum*, whilst *Anodonta cygnea*, *Unio pictorum* and *Limnaea auricularia* occur only in the river and the two small lakes of the district.

Two species are frequently encountered in the closed ponds but are absent from the river, viz. *Planorbis nautilus* and *Sphaerium lacustre*. The presence of these species in what the author aptly describes as ecological slums and their absence from favourable habitats affords as interesting a problem as the occurrence of *Limnaea palustris* in habitats that are either very good or very inferior. Dr Boycott points out that the available data do not favour explanations either on the basis of competitive seclusion or the idiosyncracies of dispersal, and it is suggested that the importance of otherwise unfavourable habitats may be the absence of some inimical biological factor.

The temperature, muddiness, character of mud, and food supply, obtaining in closed ponds are briefly considered as causes of the indifferent character of this type of habitat and the conclusion arrived at is that opacity of the water and the meagre supply of oxygen are the chief factors concerned.

We have here only adumbrated the author's main conclusions but the value of this contribution is as much an outcome of the suggestive consideration of the problems, and ecologists will look forward to the publication of the detailed results of which this is a preliminary account.

E. J. S.

EDITORIAL NOTE—PUBLICATION OF NOTICES OF ECOLOGICAL PAPERS

The Editor and Council have recently had under consideration a comprehensive scheme for publishing short notices of all ecological publications to which access could be obtained. It was widely held by members that an attempt should be made to publish an exhaustive review of ecological literature in addition to occasional longer critical reviews of individual works or groups of papers. During the first two or three years of the Society's existence the place of such a scheme was largely filled by Dr Cavers' admirable detailed summaries of papers. It was impossible to carry on this work after Dr Cavers' retirement from the editorship, and the course which seemed best was to share the work of noticing papers among those members of the Society who had easy access to the journals publishing ecological matter, restricting the length of each notice to a few lines or in the case of more important publications to a few paragraphs. Even with such a restriction an exhaustive set of notices would have occupied a very considerable number of pages each year and would thus have encroached pretty seriously on the space available for original papers. The ideal thing would have been to publish the notices separately after the style of the Physio-

logical Society and so to have left the *Journal* space intact. The Committee on Plant Physiology already contribute those Physiological Society abstracts which deal with plants, and the scheme upon which that Committee works might well have been adopted with suitable modifications by the British Ecological Society, an arrangement being concluded with the Committee so as to avoid overlapping. Such a scheme of separate publication is however impossible under present conditions owing to the cost and the restrictions on the use of paper. The Council therefore decided at its meeting in November, 1917, though with some misgivings, to go ahead with the scheme, including the abstracts in the *Journal*. Recently, however, the Editor received a letter from Dr Forrest Shreve, the Secretary-Treasurer of the Ecological Society of America, stating that the Botanical Society of America had decided upon a comprehensive scheme of publishing notices of botanical papers which would take the place of the *Botanisches Centralblatt*, and that Dr H. C. Cowles of Chicago was undertaking the ecological side of the scheme and was determined to make it as exhaustive as possible. Under these circumstances, and especially since the conditions in the United States at the present time are certainly more favourable than in the British Isles for the inception of a work of this nature, the British Ecological Society's scheme has been held up pending developments.

THE ECOLOGICAL SOCIETY OF AMERICA

A meeting of the Society was held at Pittsburgh, December 28, 1917 to January 1, 1918. The programme included meetings for the reading of papers, joint sessions with the Society of American Foresters and with the Botanical Society of America, a business session "for discussion of matters of policy in regard to membership and the establishment of a journal," an address by the President, Dr Ellsworth Huntington, reports by the chairmen of the committees on Climatic Conditions, the Preservation of Natural Conditions for Ecological Study, Succession, Economic Insect Ecology, Freshwater Fish and Fisheries and Soil Temperatures, an ecological dinner, a "smoker" to which all biologists, men and women alike, were invited by the biologists of Pittsburgh, and a *conversazione*.

The papers read ranged over a wide variety of topics, as was the case at the New York meeting of the previous year, reported in this *JOURNAL*, 5, p. 119. We have not space to print all the abstracts given, but subjoin a few that appear of the greatest interest.

W. H. Emig. "The Plant Geography of the Arbuckle Mountains, Oklahoma."

In these studies the plants were grown in glass tubes and were under constant conditions of temperature and illumination. A prepared gaseous mixture containing oxygen in concentration varying between about 0.7 per cent. and 14.4 per cent. was employed. The root growth of *Prosopis velutina* and *Opuntia versicolor*, as well as that of certain other species, in soil with unlike oxygen content, was observed. Among the results the following may be mentioned. The results previously obtained, namely, that the roots of *Opuntia* appear to require a better aerated soil for growth than do those of *Prosopis*, were verified. Growth of the roots of cuttings of *Opuntia* and of relatively long *Prosopis* roots ceases promptly in an atmosphere containing less than 1 per cent. oxygen, but if there is 10 per cent. more or less oxygen in the air of the soil root growth continues for several hours at a diminishing rate, and at length ceases. The rate of root growth at parallel soil temperatures and in an atmosphere of the same oxygen content is always greater in *Prosopis* than in *Opuntia*. The relation of the root growth of relatively young *Prosopis* plants to oxygen appears to be inconsistent, although exactly on what this is based was not learned. A certain, but relatively slow growth rate occurs in the roots of very young *Prosopis* in an atmosphere containing less than 1 per cent. oxygen. Under the same conditions the roots of *Covillea tridentata* of the same age either exhibit no growth or very little growth. Thus it is shown that the roots of young and relatively young desert plants show unlike relations to oxygen.

Henry C. Cowles. "Retrogressive and Progressive Successions in the Arkansas Sunk Lands."

The sunk country of the Mississippi bottom lands has for the most part two types of progressive successions, both hydrarch as to origin. One, of course, is the familiar flood plain succession, starting with the Sand bars and having successive belts of invading vegetation, commencing with willows and followed later by the sycamore, cottonwood, and other flood plain pioneers. Then follows a long-enduring temporary climax (subclimax) composed of bottom land oaks, hickories, hackberry, etc. The second progressive hydrarch succession occurs in cut-offs, incident to changes in the river channel. Here there develop the familiar cypress swamps, following the more primitive aquatic stages. These swamps also develop into the above named flood plain temporary climax. The earthquake of 1811 caused an extensive sinking of the earth's crust over vast areas of the Mississippi bottoms, thus

instituting a sudden retrogression in the vegetable development. Probably much of the area now covered by cypress swamps had reached the above noted temporary climax or even the regional climax at the time of the earthquake. Since that time it is probable that the vegetational course has been essentially progressive. This region presents a sharp contrast in the suddenness of vegetative change produced by the earthquake to the more common (and usually overlooked) retrogressive changes brought about by gradual subsidence or elevation.

Lynds Jones, Oberlin College. "The Effect of Nine Years of Protection on the Breeding Birds of the Washington Coast Bird reservations."

The study of these reservations began in the early summer of 1907, just prior to the taking effect of the act which set them aside as reservations. Then the breeding habits were extensively studied and the numbers estimated with care, for each species. Visits were made in the early summer of 1915 and 1916, when further studies were made of the same colonies of breeding birds. These studies proved that there had been a considerable increase in the numbers of certain species of cormorants, and a considerable shifting of the breeding colonies of California murres because their former breeding ledges had been appropriated by the gulls. Under normal conditions the numbers of the gulls had been restricted by the periodical raids of the coast Indians upon them. This is now forbidden under heavy penalties. These gulls feed upon the eggs and young of the other birds, and are able to drive any of the other birds from their nesting places. It would appear that the rigid protection of the birds on this coast is resulting in readjustments of the breeding birds—to the decided detriment of those which are not able to defend themselves against the gulls.

J. V. Hofman, Forest Service. "The Influence of Vegetation on Reforestation in the Cascade Mountain Region."

This paper covers briefly the influence of shrubs and annuals on reproduction, whether natural or artificial. The conclusions are based on data gathered in connection with natural reproduction studies and planting and sowing experiments during the past five years. The effect of different degrees of shading by the native vegetation on various sites such as north slope, south slope, flat, etc. is shown. The general conclusions show that shading in this region is not an important factor except at the extreme limits of either site quality or density of shade.

Edward N. Munns, Forest Service. "Some Biological and Economic Aspects of the Chaparral."

This paper embraces a discussion of evidence pointing to the fact that the so-called "true chaparral" of Southern California is temporary in its character and that tree growth existed prior to the brush and will again cover the area if given a full chance. The evidence presented in support of this view is that of the fossil deposits found at La Brea; the brush species of the north associated with the coniferous forests are also found in the south; stumps and charcoal remains of tree growth are found in dense brush areas where no one can recall such growth; trees (species of spruce and several pines) are in scattered stands in the chaparral; and plantations of coniferous trees have been successfully established. Fire has been the agency which is responsible for the decrease in tree growth and the increase in the brush areas, and if the fire rotation can be increased from its present rate to one greater than the tree rotation, trees will again come in naturally.

Clarence F. Korstian and **Frederick S. Baker**, Forest Service. "Precipitation as a Factor Limiting the Distribution of *Pinus ponderosa scopulorum*."

After compiling data from a number of cooperative Weather Bureau stations within the range of the Rocky Mountain variety of western yellow pine (*Pinus ponderosa scopulorum*) it is concluded that the amount of precipitation during the summer is a potent factor in limiting its distribution, especially in determining its lower limits and in limiting its occurrence in the Great Basin to small isolated areas and scattered individuals. Annual precipitation curves for stations within the range of the variety show a decided crest occurring during June, July or August, while such a crest is practically lacking for Great Basin stations which otherwise appear comparable.

Frederick S. Baker, Forest Service. "Native Plants as Indicators of Forest Planting Sites."

The native vegetation on a given site indicates the chief factors governing the value of that site for forest planting based on the nature of its root systems, the transpirational activity, and its place in the natural succession. However, the indicator plants react upon the site and must also be taken into consideration in determining its potentiality.

ON THE RELATIONSHIPS OF SOME ASSOCIATIONS
OF THE SOUTHERN PENNINES

By R. S. ADAMSON

(With two Figures in the Text)

Probably no series of associations has been more studied from the standpoint of primary survey than those of the silicious hills such as the Pennines, which were among the first associations to be studied in this country¹. The object of the present communication is to bring forward a few facts which have hitherto been overlooked or treated as of little importance, but which appear to the writer to warrant modification of the schemes hitherto put forward.

The associations² to be considered are chiefly those of the upper slopes and summit plateaux which have generally been grouped into the two divisions of silicious grasslands and moorlands.

Detailed descriptions of the topography and of the main features of the associations have been so admirably given by Moss and others³ that they need not be repeated here, and no full floristic lists will be given.

MOORLANDS

Three main moorland associations are generally distinguished on these hills, namely those dominated by *Eriophorum vaginatum*, *Calluna vulgaris* and by *Vaccinium myrtillus* respectively: the first occurs on the flat summits and plateaux on deep ill-drained peat, the *Calluna* moor at rather lower altitudes on gentle slopes and ridges, while the *Vaccinium* moors occur on steep rocky slopes or edges, on exposed summits and as a degradation stage of the *Eriophorum* moor when the latter has been cut up by watercourses and is drying out.

Eriophorum (Cotton Grass) "Moors" (Mosses)

The association dominated by *Eriophorum vaginatum* occupies all the broader tops above about 1000–1200 feet, occurring on deep peat which is always rather wet and undrained, though the statement⁴ that this peat is rarely less than 5 feet in thickness is perhaps a little exaggerated as there are flourishing *Eriophorum* moors on peat only 2–3 feet in thickness. The peat

¹ Smith and Moss, *Geog. Journal*, 21, 1903, p. 375. Smith and Rankin, *Geog. Journal*, 22, 1903, p. 149.

² The term "Association" is used throughout as defined by Moss in *New Phyt.* 9, 1910, p. 26.

³ Moss, *Veget. of Peak District*, 1913, and in *Types Brit. Veget.* 1911, also Smith and Moss, *op. cit.*, Smith and Rankin, *op. cit.*

⁴ V. P. D. p. 184. T. B. V. p. 288.

however is always relatively pure and free from admixture of sand or mineral matter¹. The roots of all the plants composing the association are wholly confined to the peat substratum and do not pass into the mineral soil below.

At the base of the peat there appears nearly always a more or less marked pan layer, which may be quite hard and stone-like; this pan is developed at from 3 in. to 2 ft below the base of the peat. At the present time associations of *Eriophorum* appear to be forming or extending only under quite local conditions, as in hollows representing the sites of pools or tarns. Almost all the extensive *Eriophoreta* show signs more or less advanced of degeneration and decay. This process takes various forms dependent on the causative agents and the rapidity of their action. The commonest and most rapid method is by streams cutting back into the peat and producing the series of retrogressive associations so well described by Moss². The first coloniser of the drained peat along the channel is *Empetrum nigrum*: the more widespread *Vaccinium myrtillus* follows on the drier peat. Frequently round the heads of streams the only sign of retrogression is a lining of *Empetrum*, while lower down where drainage is carried further *Vaccinium* occupies more extended tracts. This process of retrogression accompanied by removal of the peat may continue uninterrupted till the rock soil below is exposed and the original peat associations entirely replaced by grasslands generally dominated by *Nardus stricta*. The process however is not always continuous; occasionally secondary successions with recolonisation by *Eriophorum* may occur. Here the rhizomatous *E. angustifolium* is generally more abundant than the tufted *E. vaginatum* but occasionally the latter species colonises and temporarily stabilises areas of broken peat when the line of a channel alters. These secondary successions are however of very local occurrence and of no great vegetational importance.

Other methods of retrogression however occur besides that of stream cutting. Jefferies³ has described the transitions to associations of *Molinia coerulea* that occur with increase of soil aeration along the line of slow flowing streams not actually removing peat. This process though absent from the immediate neighbourhood of the Peak is very frequent on the flatter moors further north. The same author has described a succession from cultivated land leading through associations of *Molinia* to *Eriophorum*.

On the lower and more isolated hills a process of gradual drainage and drying of the peat seems in progress, and this occurs without actual removal of the substratum. The so-called transition moors⁴ dominated by *Eriophorum* and *Calluna* together which occur usually on rather steeper slopes than those occupied by pure associations of *Eriophorum* would appear to fall into this category. The change of conditions here seems exactly parallel to that occurring in the lowland moor when the gradual raising of the surface above

¹ About two per cent. Cf. **Crump**, *Rep. Brit. Ass. Portsmouth*, 1911, p. 502.

² *V. P. D.* pp. 188-192. *T. B. V.* p. 280.

³ **T. A. Jefferies**, this JOURNAL, 3, 1915, p. 93.

⁴ *V. P. D.* p. 187.

the water table by the accumulation of peat allows an invasion of *Calluna* into an association previously dominated by *Eriophorum* alone¹. Pure associations of *Calluna* on *Eriophorum* peat may occur at the bases of steep slopes rising from the *Eriophorum* plateau. Towards the edges of a plateau however the stages of increasing dryness can often be seen much more clearly. Passing from the pure *Eriophorum* association, the first stage is a lack of luxuriance of the dominant plant, an almost complete absence of *E. angustifolium* and an admixture in increasing quantity of *Scirpus caespitosus* and *Calluna vulgaris*. With increasing dryness *Vaccinium myrtillus* and *Juncus squarrosus* appear, with some *Nardus stricta* and *Deschampsia flexuosa*, though the last seems seldom more than an occasional species. In certain cases this succession

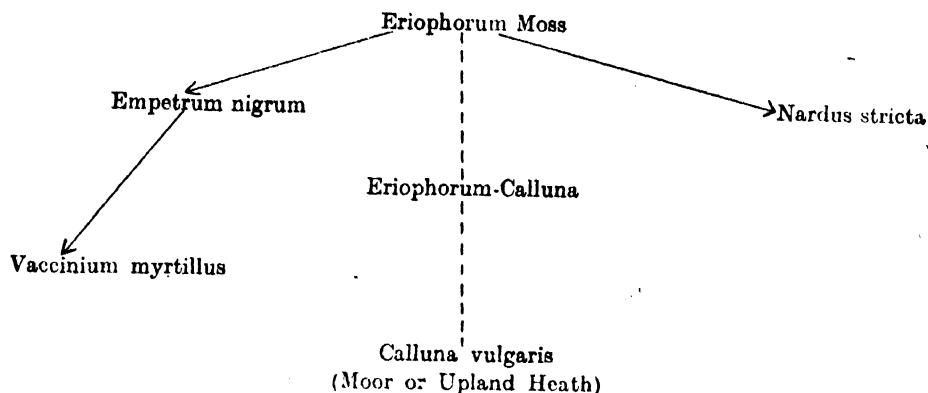


FIG. 1. Diagram to illustrate relationships of the "Oxodion" or Moss Formation. Arrows represent successions from destruction of the Eriophoretum. The dotted line represents the transition to Moor (Upland Heath).

reaches the relatively stable condition of co-dominance of *Nardus* and *Juncus squarrosus*, with *Eriophorum* existing only on the wettest parts. This association existing on peat formed mainly of *Eriophorum* remains may also be developed from peat denuded by stream cutting where denudation has temporarily ceased. Though of local occurrence in this district and best developed on the smaller and more isolated hills, it is of wide distribution in other hill districts on peats formed by various pre-existing associations².

Retrogression and destruction of *Eriophorum* associations also take place through the action of wind on isolated and projecting summits and on the crests of ridges. The wind dries the peat and causes a more or less rapid removal, even ultimately leaving bare rock devoid of vegetation. Thus occasionally on wind-swept summits vegetation is confined to small islands of peat held by *Eriophorum angustifolium*, which appears much more resistant to such conditions than *E. vaginatum*. Much more commonly however the

¹ Cf. *T. B. V.* pp. 249-50.

² Cf. *Smith*, this JOURNAL, 6, 1918, p. 1. The Nardetum referred to appears to be the same as that described by Smith as occurring zonally to the main peat mass on the Moorfoot Hills.

removal of peat is much less rapid and a series of retrogressive changes is met with closely paralleled by those occurring when drying is due to stream cutting—*Empetrum nigrum* and *Vaccinium myrtillus* forming associations on dried peat formed of *Eriophorum*. Apparently many of the so-called "*Vaccinium* summits"¹ are associations retrogressive from *Eriophorum*, though others are of the nature of typical *Vaccinium* edges and exist on thin sandy peat formed from remains of the plants composing the associations². These last are generally characterised by an abundance or even co-dominance of *Deschampsia flexuosa*, which is rare or absent on *Eriophorum* peat.

All these various forms of "retrogression" are assisted by burning, which though not regularly carried out does occur at times. Not only do the streams tend to remove peat faster but the *Eriophorum* may take some time to re-establish itself after burning and meantime allows an immigration of *Vaccinium*, *Nardus* and *Juncus squarrosus*. The two last penetrate into the moors along the lines of footpaths, which can often be traced from a distance by the difference in the colour of the vegetation.

The *Eriophorum* moor seems at the present time to represent a legacy from previous conditions dating back to the withdrawal of the ice-sheet from our hills and, with only occasional exceptions³, is not only not forming to-day but is actually being destroyed, the so-called retrogressive associations being stages of the destruction.

Calluna and Vaccinium Moors

The other moors in this district, namely those dominated by *Calluna* and *Vaccinium*, are very closely allied to one another and differ from the foregoing in several features. The most essential is the nature of the peat, which is much thinner, rarely over 1 foot and usually only a few inches, and is always much mixed with sand and mineral matter⁴. The peat is much less coherent and crumbles easily when dry. Below this thin peat layer occurs a variable thickness of soil which is much darkened and discoloured by peat, a layer termed by Crump the "sub-peat"⁵. Unlike the conditions existing on the *Eriophorum* "moor," the roots of the species composing the association here penetrate freely beyond the peat proper into this sandy sub-peat and sometimes also into the paler sand below. The two associations are very closely allied, appearing to differ mainly in their topographical relationships and to be largely controlled by the degree of exposure to wind and the minimum water content of the soil that may occur in periods of drought; *Vaccinium* being able apparently to withstand much more severe conditions in relation to both factors than *Calluna*. Thus *Callunetum* occurs on moderate slopes and the lower plateaux,

¹ T. B. V. p. 273.

² Cf. Smith and Moss, *loc. cit.* Smith and Rankin, *loc. cit.* Cf. section on *Vaccinium* moors below.

³ T. A. Jefferies, *loc. cit.* Moss, V. P. D. p. 186.

⁴ Tables, see Crump, *New Phyt.* 12, 1913, pp. 138-9.

⁵ Crump, *op. cit.*

while *Vaccinietum* occupies edges and very steep ridges, especially where rocky. Hence the latter is relatively much more abundant on the steeper western slopes of the main ridge, while on the eastern side, where the slope is more gradual, *Calluna* associations are much more prominent. Every grade of transition can be found between the two associations on intermediate types of habitat. Very steep and rocky sandstone slopes are clothed with the *Vaccinium* association, while shaly and more scree-like slopes have a mixed association in which *Calluna* and *Vaccinium* are co-dominant, if the term may be applied to what is really an open association on a very unstable habitat. In such situations both *V. myrtillus* and *V. vitis-idaea* occur either together or in alternation, and locally *Erica cinerea* may be very abundant—sometimes so much so as to lend a character to the association.

It seems probable that these two associations of *Vaccinium* and *Calluna* respectively are related to one another successionally, the *Calluna* being the later and apparently stable final stage. This will be further considered in relation to the grasslands, but some evidence can be gained from the recolonisation of burned areas¹. Immediately after a fire grasses become prominent, especially *Deschampsia flexuosa*, and also to a less extent *Nardus stricta*, but these generally form a very transitory stage and are followed and replaced by *Vaccinium myrtillus* which in turn becomes mixed with *V. vitis-idaea*, *Empetrum* and young *Calluna*. For some time an apparently stable association occurs composed of a mixture of *Calluna* and *Vaccinium* spp., but gradually the shade cast by the taller *Calluna* plants reduces the others to a quite subsidiary position. After burning has been carried out on steep slopes the surface peat is often largely removed by rain, etc., and the recolonisation succession takes a longer time. The grasses may under such conditions become much more important, even assuming temporary dominance, but they are gradually ousted and replaced by *Vaccinium* and this in turn by *Calluna*, though a mixed association may be apparently final here. The permanent associations of *Vaccinium* would thus seem to represent stages when the full succession is stopped owing to topographic or other factors.

The two species of *Vaccinium*, *V. myrtillus* and *V. vitis-idaea*, both occur in these associations but have not quite the same habitat relationships; the latter, *V. vitis-idaea*, has a more limited range of conditions. It occurs very rarely below about 1000 ft and is absent from situations much exposed and liable to considerable drought. As regards peat and water content *V. vitis-idaea* appears intermediate between *V. myrtillus* and *Calluna*, but seems better able to withstand the shade of the latter, as it is often an associate, in rather small quantity, of the typical *Callunetum*. *V. vitis-idaea* occurs but is much less abundant than *V. myrtillus* in the "retrogressive" stages of the *Eriophorum* associations.

Isolated summits and the tops of edges in the *Calluna* moor frequently

¹ Cf. T. B. V. p. 277. V. P. D. p. 178.

show a change of vegetation, the *Calluna* being replaced by *Empetrum nigrum*, especially when the soil over the solid rock is very thin. Such *Empetrum* ridges are a characteristic feature of many of the lower hills and occur not only in this district but equally in other hill regions under similar conditions.

SILICIOUS GRASSLANDS

Though exceedingly different from the moors in appearance every grade of transition can be traced between the two. The differences in habitat, also, are very slight. The peat layer in grasslands is usually much thinner, being rarely over 6 inches and often scarcely discernible as a definite layer. The sub-peat also is much less distinct, though with very rare exceptions a dark peat-coloured layer rich in acid humus occurs; but every gradation can be found from a mineral soil with dark acid humus to the condition of a surface peat overlying a sub-peat layer. The grasslands fall into two distinct groups, first, a purely lowland grassland, a permanent pasture, that owes its existence almost wholly to cultivation in the form of liming, manuring and continuous grazing, and secondly an upland series of grasslands that are quite uncultivated. These two can be distinguished easily from one another even at a considerable distance, by the colour and type of surface: the lowland cultivated grasslands are a fresh green as opposed to the dull grey or brownish green of the uncultivated areas. The lowland grasslands also have a smooth surface, while the upland pastures are typically built of small tufts or tussocks.

Not much need be said here about the cultivated grassland associations. They are dominated by a variety of grasses, mostly with flat leaves; the most generally distributed species being *Anthoxanthum odoratum*, *Agrostis vulgaris*, *Festuca ovina*, *F. rubra*, *Cynosurus cristatus*, *Poa pratensis* and *Briza media*. The accompanying flora is poor as compared with the meadows in the plains but rich as compared with the upland associations¹. Apart however from these permanent pastures of the hill slopes a natural grassland occurs in places apparently never affected by cultivation, which differs markedly from the upland pastures. This grassland, which is referred to by Moss as mixed silicious grassland², is generally dominated by *Agrostis vulgaris*, *Festuca ovina* and *Anthoxanthum*, with a small form of *Poa pratensis* very abundant, though in many cases the grasses of the peaty upland, *Deschampsia flexuosa* and *Nardus stricta*, are very abundant or even locally dominant. This *Agrostis-Festuca* grassland occurs on a rather different soil, as peat is not developed except where the upland grasses are present, and the humus in the soil is much less markedly acid. It is an association of variable composition, and somewhat lengthy lists might be given of its components³: much of it undoubtedly exists on the site of original woodlands now destroyed. Direct evidence of this is not lacking in many cases, in its proximity to existing woodlands, in the frequent

¹ List, *V. P. D.* pp. 202-3, though this includes quite lowland species.

² *V. P. D.* p. 112.

³ *V. P. D.* pp. 112-13.

presence of isolated trees and bushes, chiefly *Betula pubescens* and *Crataegus*, and further in the presence of a number of species characteristically shelter-loving which are scattered through the association, and among which may be mentioned *Anemone nemorosa*, *Vicia sepium*, *Viola riviniana*, *Oxalis acetosella*, *Ajuga reptans*, *Holcus mollis* and occasionally *Scilla nonscripta*¹. This type of grassland however is of very limited extent, while the upland grasslands cover exceedingly wide areas on the lower slopes of the hills. The upland grassland is perhaps the most extensive vegetation type in the district and occurs at altitudes from about 400 feet up to 1700 feet or even more, and equally on very steep slopes and nearly level ground. It is generally treated as one association with a number of facies²; but some of these at any rate have such marked and constant habitat and successional differences that it would seem more natural to regard them as distinct associations even though occurring within such narrow topographic limits as to prevent their representation on the usual scales employed for general vegetation maps.

The upland grassland is usually considered to be dominated by *Nardus stricta*, but this is largely a generalisation from the appearance of the association as seen covering whole hillsides where the large tufts of this grass, especially in winter, are much the most prominent feature. The composition of the grassland, however, varies considerably with variations in the habitat and especially with the amount of peat that is present. On relatively gentle slopes or level ground where peat can accumulate and where surface drainage is poor without actual stagnation of the soil water, *Nardus* becomes truly dominant almost to the exclusion of all other species. In such situations peat may be present to a depth of as much as 6 inches. On rather steeper slopes or where the peat is thin and drier, dominance is shared by *Deschampsia flexuosa*, which fills the interstices between the tufts of *Nardus* and is not only frequently numerically far more abundant but owing to its freely branching superficial rhizomes has as much or even more controlling effect on the other species composing the association. Again on steep slopes where only a thin peat is present which is liable to periods of great drought, or at low levels and in very exposed situations, *Nardus* is often quite absent and *Deschampsia* is dominant alone. In fact, though frequently occurring together, these two grasses in this district have not by any means identical habitats; *Nardus* flourishes on a more peaty soil with an imperfect surface drainage or other supply of continuous moisture, while *Deschampsia* dominates the less peaty and drier soils. The distribution of the two plants is well brought out in their topographic relations on many of the lower grass-covered hills: the dip slope with its gentle contours is covered by grassland dominated by *Nardus*, the escarpment face by *Deschampsia* alone, while below the "edge," on the more moderate slope, co-dominance of the two plants occurs³.

¹ Full list, *V. P. D.* pp. 110-11.

² *V. P. D.* pp. 106 et seq. *T. B. V.* pp. 132-135.

³ Cf. **H. Jeffreys**, this JOURNAL, **5**, 1917, p. 129.

Before, however, the relationships of these grasslands to the moors and the lowland associations are considered some of the other types of associations or "facies" may be mentioned very shortly. Much the most important in regard to area of ground covered is that dominated by or characterised by a great abundance of the bracken, *Pteridium aquilinum*. This plant occurs not only in the grassland but also in the associations of *Calluna* and *Vaccinium*. It is rarely found in quantity on exposed hillsides except at low levels; but communities of it ascend along valleys and gorges, from the sides of which they spread out, reaching as much as 1700 feet. At the lower levels, below 800 feet, where whole hillsides may be covered by sheets of bracken¹, its situation probably represents the site of original woodlands or a direct extension from such a site. But in its upper regions communities of this species occur considerably above the present forest limit and in situations which were probably not under woodland in historic times. The communities, again, often appear to be rapidly spreading and extending their area even at these higher altitudes. The most probable explanation is that the plant started from original woodlands and has spread out, mainly by vegetative reproduction, along the more sheltered valleys where the general conditions to some extent simulate those of a forest. From such situations the communities have spread out, where possible, at the expense of the pre-existing associations. This spread has been most rapid on the deeper sandy soils derived from the softer sandstones. On shallow sands and on shale soils bracken communities are much less extensive and often the plant fails to dominate the situation. These communities may have the bracken dominant and occurring quite pure, in which case they spread and gain ground largely by the destruction of light-demanding species, by shading and by the mass of dead fronds which decay somewhat slowly². The rhizomes penetrate below the peat surface, and even in many cases below the sub-peat. The bracken spreading in this way advances into grasslands or moorlands³ and may entirely drive out the original association: in other cases it only attains the condition of fronds scattered through the association. The spread is undoubtedly assisted considerably by the periodic burning of the moorlands: the rhizomes are generally unaffected, and as burning takes place in late winter or early spring the plant is able to spread and obtain a firm hold before the *Calluna* or *Vaccinium* can become re-established. Thus these bracken communities are regarded as definitely invasional into a distinct association rather than as facies of the grasslands. They take no part in the normal successions of which the grasslands form a stage, but are derived from previous woodland communities, though they may have spread far from their original starting point.

¹ V. P. D. p. 108. fig. 15.

² On spreading of bracken communities, cf. Farrow, this JOURNAL, 3, 1915, p. 223, and especially 5, 1917, p. 163. See also H. Jeffreys, this JOURNAL, 5, 1917, p. 142.

³ In one locality the plant has been observed colonising the edges of a retrogressive *Eriophorum* moss.

Local developments of other associations occur in the grassland area in flushes, springs and in wet hollows. The only one of these that calls for any mention here is that dominated by *Juncus effusus*. There are really two distinct types of habitat where this plant is a dominant or at any rate a very abundant species¹, namely the characteristic *Juncus* swamp round the heads of springs which is of small extent on the southern Pennines as compared with the hills of the more northern counties, and secondly a drier *Juncus* association referred to by Moss as the *Juncus* facies of the *Nardus* grassland. This association occurs along channels where water flows in wet seasons and on slopes flushed by intermittent springs. In either case the soil water is more or less well aerated and as a rule the peat layer is quite thin. The rush is rarely sole dominant but is associated with *Nardus stricta*, *Deschampsia caespitosa*, and where the rate of flow of water is less, with *Molinia caerulea*. All transitions can be traced between a typical *Juncus* flush and a wet *Nardus* grassland, depending mainly on the degree and constancy of the flushing. Such *Juncus* associations seem quite separate from the grasslands in their dependence on regular flushing and the consequent partial neutralisation of the peat. In the *Calluna* moor a flush line frequently has a zonal arrangement of the two associations, *Juncus* in the wetter parts and *Nardus* further out. There is no evidence of any successional relationship without marked changes of the habitat factors.

RELATION BETWEEN GRASSLAND AND MOORLAND

Every grade of transition can be found between the grassland and the *Calluna* and *Vaccinium* associations, correlated with gradual increase in the amount of peat in the soil. The grasslands nearly always have *Vaccinium myrtillus* as a constituent species, either thinly scattered or forming local societies. The situations occupied by these societies mark the positions where the most definite and largest peat deposits occur. On the less steeply sloping grasslands *Nardus* is frequently associated with *Calluna* and *Empetrum* in addition, and as peat gradually accumulates in larger quantities these plants tend to assume dominance over the grasses and gradually to drive them out altogether. This increase in the moor plants certainly appears to depend on grazing as one of its chief factors: of two adjacent and apparently identical areas a striking difference occurs when one is pastured by sheep and the other not, the latter showing a much greater development of the moor plants and with them usually of peat. A striking feature also is the sharp line of demarcation that often occurs along a wall which marks the limit of sheep grazing, no grasslands occurring above, and below nothing else.

Just as there is a gradual transition between the grasslands and the moorlands so equally every stage can be found of change from the cultivated permanent pasture to the natural associations on acid peaty soil. Where one of these pastures is left uncared for and not much grazed, the first change seen

¹ Cf. V. P. D. pp. 108 and 148.

is a very great increase in the quantity of *Deschampsia flexuosa*, which rapidly assumes dominance; the more mesophytic grasses are either suppressed or reduced to isolated islands of decreasing size. The *Deschampsia* quickly develops a thin peat layer and when established soon becomes associated with the more markedly peat-loving plants—*Vaccinium myrtillus* and *Nardus stricta*, except in very dry places. When the surface drainage is poor *Nardus* gradually spreads, ultimately to the exclusion of *Deschampsia*. Even in derelict arable fields this reversion to the peaty associations can be seen. In deserted fields with furrow marks it is common to see the summits of the ridges marked by *Deschampsia* associated with more or less numerous tufts of *Nardus*, while the furrows, which are moister and become acid less rapidly, still retain the green mesophytic grasses.

These various facts, which can be traced with more or less completeness on any of the hill slopes, very strongly suggest a successional relationship of the acid peat-forming associations. The first stage, with the thinnest and least definite peat layer, is the *Deschampsia* grassland. As peat accumulates this association gives place to one of *Nardus stricta* and this in turn to one of *Vaccinium myrtillus* or *Calluna vulgaris* which appears to be the stable end stage of the series. On very steep slopes where only a thin peat layer can be formed which is liable to extremes of drought the succession passes directly from *Deschampsia* to *Vaccinium*, which is the end stage here. Exactly the same succession can be traced in the degeneration of woodlands in the district. Here again the starting point—an assumption of dominance by *Deschampsia flexuosa* on an acid substratum, is followed by the various other stages as traced above. Here owing to the additional factor of shade the *Nardus* association is often eliminated and that of *Vaccinium myrtillus*, a shade-tolerant species, is of much more prominence. Thus the subassociation of the *Quercus sessiliflora* wood with much acid humus¹ described by Woodhead as a “xeropteridetum”² would not be regarded as a true association any more than the Oak Birch Heath³ can be or the open forms of scrub⁴, but as a transition containing elements of two separate and distinct associations. In the case described the acid peat associations are invasional in the woodland.

The present distribution of the various associations that are thus regarded as successional related is largely the result of sheep pasturage and especially of its concentration by fencing. Smith and Crampton⁵ have already pointed out the effects of sheep on moorlands and Farrow⁶ has proved that the transition from *Calluna* to grassland on the East Anglian Heaths is the same effect carried out by rabbits.

It is most probable that the greater part of the present grassland area was originally covered by *Calluna* and *Vaccinium* associations, much of which

¹ *T. B. V.* pp. 127 and 130. *V. P. D.* p. 56. ² *Journ. Linn. Soc. Bot.* 1906, p. 347.

³ *T. B. V.* p. 100.

⁴ **Tansley**, this JOURNAL, 1, 1913, p. 279.

⁵ *Jour. Agric. Sci.* 6, 1914, p. 14.

⁶ This JOURNAL, 4, 1916, p. 57, 5, 1917, p. 1.

would have invaded and replaced still earlier forests. The destruction of these moors has been brought about by grazing and by flushing. Originally, then, *Nardus* and *Deschampsia* associations would have been confined to stream or flush channels where the accumulation of peat beyond a certain point is prevented¹. In such situations, indeed, in the upper and uncultivated parts of the hills, these associations occur at present. This will also explain the existence of *Nardus* associations on peat of 4–6 inches in thickness which contains the remains of *Calluna*: the succession has been stopped and has reverted to an earlier stage under the influence of grazing and periodic firing.

This whole series of associations, including both the silicious grasslands and the *Vaccinium* and *Calluna* moors, seem very closely allied to the heaths of the lowlands and the South² both in their habitat relationships, notably the development of a sandy impure peat layer through which the roots penetrate into the underlying soil, and also in the way in which they invade and gradually destroy woodlands, or neutral grasslands. In fact exactly parallel series of stages can be traced on these hills and on the sandy tracts of heathland in the South of England, though under the climatic conditions of this district the peat formation is much more rapid and reaches a greater thickness than in the lowlands, and many floristic differences occur.

The grouping of these grassland and moor associations into two formations³ would seem unnatural and arbitrary: not only are the two connected by every gradation but all exist under habitat conditions differing only in degree and not in kind. Reasons have been given above why the *Deschampsia* and *Nardus* associations should not be regarded as associations derived from oak woods but as invasional in them and causing the destruction of the forest. In being associations arising on the destruction of the forest they can be considered as retrogressive from the oak wood association, but the habitat conditions have meanwhile altered so much as to separate them completely. They can, in fact, be no more considered with the woodlands than the grass-heath or *Calluna* heath of the South can be treated with their associated oak woods. These last two are treated as separate⁴ but their differences are no greater than those separating the associations considered here.

The associations of the deep peat of the summits, however, would appear essentially distinct both in origin and development, though the close similarity in the substratum, an acid peat in both cases, gives a considerable resemblance in floristic composition and in growth forms.

It is probable that the retrogressive stages following on the destruction of the *Eriophorum* moor should be looked on as invasions of the more modern and vigorous succession series. This series thus invades and replaces the associations both at its lower and upper altitudinal limits, though in the latter the

¹ Cf. **Smith** and **Crampton**, *loc. cit.*

² *T. B. V.* chs. v and xii.

³ *T. B. V.* ch. iv.

⁴ *T. B. V.* chs. iii and iv.

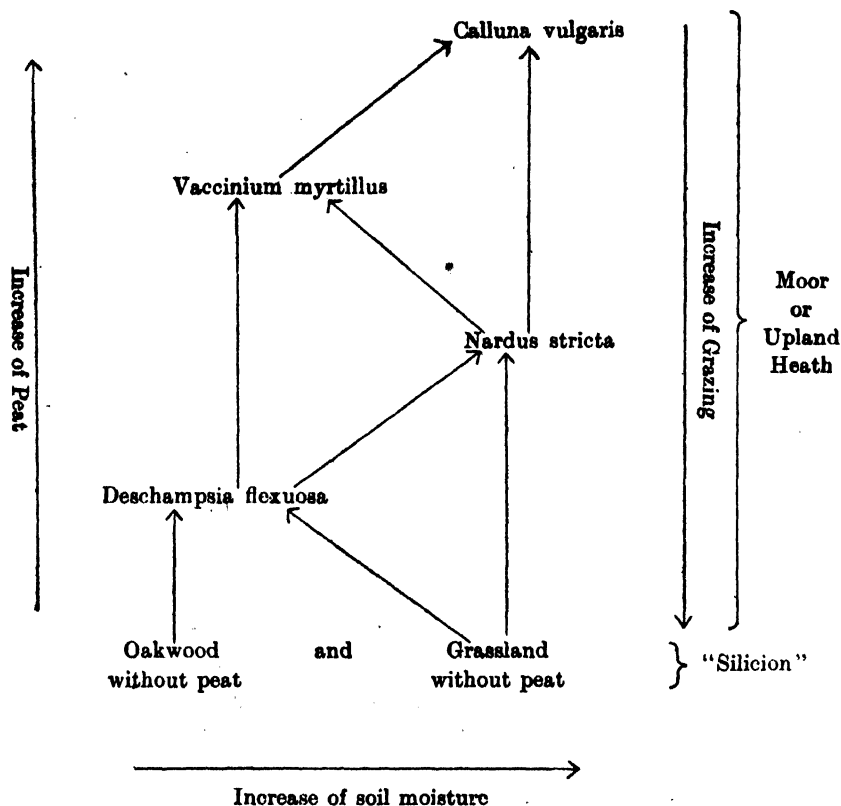


FIG. 2. Diagram to illustrate relationships of the Moor or Upland Heath Associations. Arrows represent lines of succession.

purely physical agents have a much greater share in the destruction of the existing vegetation.

From the above it would appear that the formations suggested by Moss¹, the *Silicion* and the *Oxodion*, must be somewhat modified in that the *Deschampsia* and *Nardus* associations are quite separate from the other associations of the "silicion," and, with the *Calluna* and *Vaccinium* associations, are equally to be separated from the *Eriophorum* moor. It is striking that Moss himself indicates clearly the last line of separation in his table of relationships², where the connections between the grasslands and the *Calluna* and *Vaccinium* moors are marked, but none between these and the *Eriophorum* moor. In place of two formations it seems necessary to recognise three; first that on silicious soils without peat to which the term *silicion* might well be applied, and of which the *Quercus sessiliflora* wood marks the chief association, secondly that on an acid but not stagnant or saturated surface peat with a chief association dominated by *Calluna vulgaris*, and finally that on the deep wet peat of the summits where the peat is generally more or less saturated and the water

¹ V. P. D. pp. 216-17.

² V. P. D. p. 217.

rather stagnant. This last formation is represented here in its stable phase by the *Eriophorum* moor. The second of these formations is progressive at the present time and frequently invasional, though itself invaded by *Pteridium* associations derived originally from woodland. The third formation is almost always in the condition of more or less rapid destruction and is best regarded as a relict from previous conditions dating back to the retreat of the ice-sheet. The wet flush associations belong to a fourth formation.

SUMMARY AND CONCLUSION

To summarise, the plant associations of the district fall naturally into three main groups, two of which have been treated of specially. First the associations of the summit plateaux which are on very deep wet peat, and of which the general dominant is *Eriophorum vaginatum*. This association is at present generally in a condition of decay and replacement by other associations. With few exceptions *Eriophorum* moors are not forming at present but represent an end stage of a series commencing in post-glacial times. This is the Oxodion or Moss Formation.

Secondly on the hill sides and lower hills, on thin impure peat through which the roots penetrate, associations occur dominated by *Deschampsia flexuosa*, *Nardus stricta*, *Vaccinium myrtillus* and *Calluna vulgaris*. These are stages in a succession, the *Calluna* phase being the final or chief association. These associations are invasional not only on woodlands and grasslands, either the cultivated or natural pastures of the lowlands, but also on the ground prepared by the drainage or destruction of the *Eriophorum* moor. In the former invasion a regular succession series is passed through. The present large extent of the earlier phases of the succession, the grasslands, is due to a large extent to sheep rearing.

Invasional associations of *Pteridium aquilinum* occur among the foregoing, having spread upwards along sheltered valleys from original woodlands.

Finally it may be mentioned that local names show that for practical purposes a separation on the lines suggested is very old. The term "moor" is not used for the deep peat associations of the summits, which are termed "mosses," while "moor" is applied to both the *Calluna* and the grassland areas.

A FOX-COVERT STUDY

BY REV. E. ADRIAN WOODRUFFE-PEACOCK

Poolthorn Covert, the history of which is fully known, is situated in the parish of Cadney-cum-Howsham, North Lincolnshire. It has an area of about ten acres, and was laid out in the year 1797, according to the Brocklesby Estate Office books. It lies on the eastern boundary of Cadney township, but in the middle of last century, at a date unknown to me, was extended two acres to the east, by a pure planting of Blackthorns, into the western side of Howsham township. On the authority of the late Mrs Hannah Abey (1803-1894) a native of this place, who was a lover of nature, this covert was planted on "rough grass common pasture, with Hassocks (*Deschampsia caespitosa*) in places. It was trenched for the purpose of draining just before," i.e. the ground was never under cultivation previously in human memory.

I. THE SOIL

This covert stands on two soils of widely contrasted floral sympathies. Its northern face, and about one-sixth of its area, are on thin Very Chalky Boulder Clay, that is to say—for I have had to distinguish them clearly all over this county for botanical purposes—on the basement bed of the Chalky Boulder Clay, which in some cases is practically Chalk removed to another spot by ice-action. On this bed all the true Chalk species can grow, if they once get a footing, as *Orchis pyramidalis*, *Plantago media* and *Ranunculus auricomus* f. *depauperata* have at times done in this covert. The other five-sixths are on retentive Kimeridge Clay, with its characteristic local fossil *Gryphaea dilatata* Sow., abundant in the covert. The wood stands quite isolated, there is no other covert within a mile, on an incline, the dip being to the south; and its wettest band is therefore just below the junction of the Very Chalky Boulder Clay, a porous sipping bed, with the underlying waterproof Kimeridge Clay.

II. THE PLANTING OF THE COVERT

This covert was planted in 1797, my friend, Mr W. B. Havelock, the Head-Forester at Brocklesby, tells me. In all 102,120 trees were used in planting and in renewing the next season as follows:

Oak (<i>Quercus pedunculata</i>)	49,000.
Spruce (<i>Picea excelsa</i>)	18,000.
Sycamore (<i>Acer pseudo-platanus</i>)	9,000.
Ash (<i>Fracinus excelsior</i>)	8,200.
Privet (<i>Ligustrum vulgare</i>)	7,400.
Silver Fir (<i>Abies pectinata</i>)	5,000.

Mountain Ash (<i>Pyrus aucuparia</i>)	1,600.
Larch (<i>Larix decidua</i>)	1,000.
Birch (<i>Betula alba</i>)	1,000.
Holly (<i>Ilex aquifolium</i>)	1,000.
Wych Elm (<i>Ulmus montana</i>)	700.
Spanish Chestnut (<i>Castanea sativa</i>)	120.
Willows (<i>Salices</i>)	100.

There were thinnings in the early years of the century, "the oldest inhabitant" told me—she was born in 1803; but nothing has been done for the last fifty seasons. On this retentive soil, Kimeridge Clay—for the Very Chalky Boulder Clay is too shallow in this covert to influence the main-crop growth at all—the main crop though 120 years old, is not nearly ripe yet. The late Mr Spencer, of Market Rasen, the largest of our local wood buyers, told me: "The trees of Pepperdale on the Chalky Boulder Clay grow twice as fast as at Poolthorn on the Kimeridge Clay, but are not worth more than half the money when grown." Poolthorn at present looks like requiring another 100 years to reach full maturity.

III. THE PLANTED SPECIES STILL EXTANT

One hundred and twenty years is a long gap even in the lifetime of a covert, so there have been many changes since the original planting, for such a selection of species as was made at first would not be justified by an educated forester to-day. We have learned something, if only a trifle, in the last 120 years.

Picea excelsa is still there, but only just exists. As its roots are only in the upper surface soil, it is often wind uprooted, and its wood is valueless.

Acer pseudo-platanus grows well, and is a free seeder. The ground in the less fully canopied places is often wholly carpeted with its young seedlings six to twelve inches high. See under *Fraxinus* about growing and dying, for *Acer* is just the same. Under its deepest shade only *Circaea*, *Nepeta* and *Urtica* grow.

Betula alba is there still, but never a seedling grows.

Fraxinus excelsior is healthy and a free seeder. In the more open canopied parts, it grows up till it is ten to fifteen feet high, and then dies from over-shadowing. The same species grow in its shade as in that of *Acer* above.

Larix decidua fails.

Ligustrum vulgare only does well on the ride sides.

Prunus spinosa does well in places on the ride sides, much better in the Blackthorns where there are no over-shadowing species. It can obtain a footing on the Kimeridge Clay but not on the Very Chalky Boulder Clay.

Pyrus aucuparia is now only on the Very Chalky Boulder Clay, on the ring-ride side. It seeds freely too.

Quercus pedunculata is the main crop species of the covert. The oaks will make the best of wood some day. In its shade all the *Acer* species, along with *Geum*, *Rumex* and *Geranium*, can grow.

Salix alba is now practically only round the old pond on the Kimeridge Clay, and failing there from oak over-shading.

There was one tree of *S. caprea* by the side of the Blackthorns, but it has gone these twenty years. It was on Kimeridge Clay, and was no doubt wind sown.

S. cinerea is now confined to the Very Chalky Boulder Clay, and ride side.

Ulmus montana is doing well and follows the ash as that follows the oak in numbers. It is the same as *Fraxinus* in the matter of growing up and dying.

IV. THE STOCKING OF THE COVERT

The species found in this covert to-day are easily divided into three classes, (1) those that were on the ground at the time of the afforestation, i.e., before the parish was enclosed, (2) those introduced then, (3) those which have drifted to it since. There have been considerable fluctuations, produced by several causes, since 1891, when I became Vicar of this parish, and began to take full notes of the circumstances and species found.

These opportunities for change by new conditions may be summed up as follows:

(a) The Blackthorns have been twice cut down wholly to the ground. This opening of the soil to light and air allowed of the advent of many outsiders for a time, as a clean cutting always does in woodland.

(b) Another potent cause of local change was the underwood cutting of the smaller trees and bushes of the older part of the covert. This gave a chance to a few outsiders to flourish for a limited period. It was, however, more of an opening for lowly underwood plants, such as the two common violets, and the Enchanter's Nightshade (*Circaea*), with other species, which took full advantage for the time of the opportunity given, so that I have seen acres of ground purple with *V. odorata* and *V. Riviniana*, where they cannot grow now.

(c) The next cause was the most unusual, and in its way the most potent influence of change at work. It was the presence, for some ten years, of "clouds of starlings," which used the Blackthorns as a roosting place—but never the other part of this covert. They were rightly called "clouds of starlings," for in the distance they were like a dark thunder cloud, or clouds, if they were in sections, on autumn afternoons. I have never met with a standard by which the number of birds in such multitudes can be estimated, and have vainly sought to find one. They could cover a ten acre field with a trifle of their vast flights sitting closely on the ground, as I have seen them do for some unknown reason, till it was absolutely black. I am on the safe side, when I say, that there were more than 1,500,000 in these sittings. There may have been more than thrice that number on one special day. At times of great stress this portion of the covert would not hold them, and flights late in the evening had to wing away to other gathering grounds unknown to me. On these evenings of great numbers healthy Blackthorn branches and bushes would suddenly crash down

under the united weight of many birds. Before they came to Poolthorn Covert they used Pepperdale Covert, a mile and a half away on the northern side of Howsham township. This covert was planted in 1801, and was cut down mature about ten years ago. There they killed the whole of the Blackthorn undergrowth by (1) their united weight, and (2) excreta. The main crop oak did not suffer in the least, and the ash only indirectly from their presence. Two species of woodpeckers at that time inhabited Pepperdale Covert—the Green (*Gecinus viridis*) and the Greater Spotted (*Dendrocopus major*). The starlings, I found, took possession of the nesting holes of these birds, early in the season, as fast as they made them, and caused many more borings to be undertaken than would have normally been the case. These in the end mean the destruction of the tree chosen for them, from fungus growth (*Polypori*). As the game was driven out of Poolthorn Covert by the aroma of their dung, and the Blackthorns nearly destroyed by their weight and excrement, this portion of the covert was cut down to save it from total destruction like the undergrowth at Pepperdale Covert. This effectually drove the birds from the parish.

(d) There are now two rides through the covert, N. to S., the old central one, and the Blackthorn Ride, i.e., part of the old ringing-ride between the old covert and the Blackthorns. There is a ringing-ride also round the entire covert, old and new parts together. Footpaths pass through the two central rides, and another along the N. side of the ringing-ride of the old covert from the hunting gate on the W. to that on the E. There are four of these hunting gates at the four corners of the old covert, and a large wood gate in the centre of its N. hedge. These footpaths and gates are causes of frequent and regular seed contamination from the outside. Two modes of carriage can be detected, (a) mud carriage on (1) boots and (2) cart wheels, and (b) clothes carriage. These should be carefully distinguished for field work or mistakes will be made, though in the end they produce the same effects as regards the covert—the introduction of fresh species.

(e) Another cause of change at work has been the state of the hedges. Sometimes they have been allowed to grow high, overshadowing the ring-ride, and so destroying *Orchis pyramidalis*, *Plantago media* and other species. At other times they have been cut low as now. The full light, or its modification to any extent, at once tells on the ring-ride as a powerful influence—not, however, more than on the old central ride of the covert, which has lost *Polygonum Hydropiper* by the closing in of the *Acer Pseudo-Plataeus* canopy these ten years. At present—for I regret that my notes are not as full as they should be, as I have no standard by which to work—where the central ride is darkest of all from *Acer* over-shading, three species only are found:—*Urtica dioica*, *Nepeta glechoma* and *Circaea*. Where it is a trifle lighter, *Geum urbanum*, *Rumex nemorosus*, and a drawn up, pale flowered form of *Geranium Robertianum*, which is generally carried as seed on shooting stockings, appear.

Where it is a little lighter still *Listera ovata* grows, and *Arctium minus* can just exist. Where it grows lighter still, *Galium Cruciata*, *Prunella* and *Ranunculus repens*, which in such cases may have a leaf miner, are in evidence. In the lightest part of all, *Agrimonia* and *Spiraea ulmaria* are first discovered. All these species are "drawn up" till they receive the amount of light they normally can survive under.

(f) Another cause of local sudden change was an unusually high gale in 1893, which blew down many of the largest Spruces, making wide gaps in various parts of the wood, and thus causing a vast growth of *Urtica dioica*, *Rumex nemorosus*, *Unicus lanceolatus*, *Epilobium angustifolium* and other species.

(g) A vital matter too for isolated coverts which have not yet obtained all the true woodland species is the presence of shooting parties annually, though only occasionally, from October to February. Their boots, but more especially their clothes, when they are moving from covert to covert, with a large party of beaters, are the means of importing new species. Some workers might consider this a matter of trifling importance. A friend of mine in the south absolutely declined to believe that this cause could be "anything but an infinitesimal influence." As we rested lunching by the covert side, we made a superficial examination of his clothes and shooting stockings, as he sat on his walking-stick seat. They were discovered to be carrying, after a visit to the outside of three other coverts and certain intervening stubbles and root crops, seeds of the following species:

<i>Arctium majus</i> (coat),	<i>Geum intermedium</i> (stockings) (this hybrid
<i>Bromus ramosus</i> (coat),	is fertile),
<i>Bromus sterilis</i> (stockings),	<i>Geum rivale</i> (stockings),
<i>Galium aparine</i> (stockings),	<i>Geum urbanum</i> (stockings),
<i>Galium tricornu</i> (stockings),	<i>Ranunculus arvensis</i> (stockings).

A modest and by no means large or normal contribution from the stubbles, hedges and coverts he had visited, to a freshly laid out covert, for instance! The mud on his boots was not examined. "O, my man would have removed all these to-night," he reasoned. "But you are here by this covert perhaps sowing some of them before your man gets his chance," it was urged. An argumentative man is hard to convince against his will. At the very next shoot, however, he was brought to reason. His eyes fell on me, as he stepped from his dog-cart, and he called out cheerily, "A guinea for every kind of seed you can find on me to-day before we start—the County Hospital shall have it." A search in the flue of his shooting jacket's inner and outer pockets gave the following seeds—not all of them then fertile, I should judge, from experience in such matters: *Arctium minus*, *Avena fatua*, *Centaurium umbellatum*, *Circaea lutetiana*, *Galium aparine*, *Holcus mollis*, *Hordeum vulgare*, *Phragmites vulgaris*, *Poa pratensis*. There were others, but "too rubbed" to be clearly distinguished.

The County Hospital, of which he was one of the Honorary Managers, never obtained nine guineas in a simpler way.

So potent is this means of dispersal that I prepared my field coat pockets, by a careful turning out and flue hunting, before I went into Howsham Wood on August 3rd, 1906. The following morning I again examined my pockets to find three species of seeds: *Geum urbanum*, *Juncus glaucus* and *Cerastium glomeratum*. All fairly lowly growing species, which had reached my inner pockets by some means unknown to me. *Cerastium glomeratum* did not grow then in this wood. I must have picked it up on the way there. In other words, in a four hours' walk, the seeds of three species had found their way into my pockets by some means—no doubt by being jerked up by the elasticity of their stems as my shooting boots came into violent contact with them near to the ground. The fact is worth recording. In this way I once picked up a seed of *Medicago denticulata* on the band of my stocking without observing the growing plant.

(h) The seeds brought into a covert with barley and other stubble rakings and with foreign wheat refuse used for feeding pheasants is another cause of additions, which need hardly be referred to in this JOURNAL. The species introduced in this way are so apparent and this article so long that I have not added them to it at all.

V. MEANS OF DISPERSAL

The means of carriage I have observed in direct action at Poolthorn Covert in twenty-six years are the following:

(a) Wind, (b) Mud, (c) Birds, (d) Clothing, Hair and Fur, (e) Ducks.

(a) *Wind*. This is the commonest means of transport, but one of little importance in the special case we are considering—that is, a planted wood surrounded by tilth and grass. It does act however even here, as I have often observed in the case of many Compositae and Epilobia. I have seen the seed of two species arrive in a sou'wester in early October, both taken in a butterfly net which had been carried there for the purpose. They were *Chrysanthemum Leucanthemum* and *Epilobium angustifolium*; but both were already there.

(b) *Mud*. This takes two forms, that (1) on boots and (2) on cart wheels, and is a constant cause of contamination with the species of the tilth—the carr (cultivated peat) especially—named below. The right cause can nearly, but not quite always, be detected from their position on or by footpaths or cart ruts. "Wet boot carriage" cannot be distinguished from it in the field, though it is much more easily observed on one's own person, both in the case of seeds which give out mucilage, and those which have no gumminess when wet.

(c) *Birds*. By this all-covering word, I wish to imply more than can be named here at present, classing as birds all non-water fowl. Two species especially must be named, for their work is clearly seen at Poolthorn Covert

—the starling and the blackbird. When I speak of the starling, I mean that species and it alone. When I say the blackbird, on the other hand, I mean that species and the rest of the common British Turdi. It would be ridiculous and most misleading to speak in any other way, for as a labouring-man observer pointed out to me in his own language many years ago, “the blackbird does nine-tenths of the work which may safely be attributed to the Turdi, especially in their youthful first autumn months when thrush-like in markings¹.”

(d) *Clothing, Hair and Fur.* The clothes of men and hair and fur of animals are fruitful sources of seed carriage. I cannot go fully into the matter here. *Arctium* is the species most commonly carried by mammals and the larger covert birds.

(e) *Ducks* are hardly worth naming in this paper. There is only one shallow pond in the covert, which is never duck-visited now; it is too much over-shaded by trees.

VI. THE SMALLER COMMON SPECIES

The species that have been in evidence since 1891, when I first studied this covert, are as follows:

Acer campestre doing well on the Kimeridge Clay in the S. ringing-ride. It came from the S.W. to this covert along the hedges².

Agrimonia Eupatoria.

Agrostis alba.

A. tenuis.

Alopecurus pratensis.

Anthoxanthum odoratum.

} All probably on this ground when originally planted.

Anthriscus sylvestris came along the hedges or by clothes carriage?

Arrhenatherum elatius, on ground when planted.

Arum maculatum, by the hedges.

Bellis perennis, on ground when planted.

Brachypodium pinnatum, originally and now on the Very Chalky Boulder Clay.

Brachypodium sylvaticum, on the Kimeridge Clay, originally and now.

Bryonia dioica, blackbird sown, but by starlings too.

¹ Though I have botanised for over fifty years now, I have never before seen the sight which may be observed this day, October 1, 1917. The berries of hedges quite untouched, even those of *Ribes grossularia* and *R. rubrum* in the gardens, and *Pyrus aucuparia* and *Viburnum opulus* which are making the woods flame into brightness, because there is no sugar to preserve the garden fruits with, and no birds, Turdi especially, after the seven months of frost and snow of last winter, to clear them off. We have not in some parts one thrush where there were 25 last year, or one blackbird where there were 10 twelve months ago. Such is war and weather in 1917.

² Why has it not yet reached its proper soil, the Very Chalky Boulder Clay? Can it be that it is such a sunlight lover, that the northern hedge and covert side are not light enough for it?

- Carex sylvatica*, boot mud carried, in some cases even on stockings, see below.
Caucalis anthriscus, by the hedges.
Centaurea nigra, on the ground originally.
Cerastium vulgatum, on the ground originally.
Chaerophyllum temulum, by hedges.
Crataegus oxyacantha, blackbird sown.
Crepis capillaris, on the ground originally.
Dactylis glomerata, on the ground originally.
Festuca rubra, on the ground originally.
Galium aparine, by carriage of clothes.
Galium cruciata, on the ground originally.
Galium verum, on the ground originally.
Geranium molle, on the ground originally.
Geranium Robertianum, by the hedges.
Geum urbanum, clothes carried to and from this covert every season.
Hedera helix, blackbird sown.
Heracleum sphondylium, by wind drift along the hedges.
Holcus lanatus, originally on the ground.
Hordeum pratense, originally on the ground.
Hypochaeris radicata, originally on the ground.
Juncus inflexus, originally on the ground.
Lapsana communis, along the hedges.
Lathyrus pratensis, originally on the ground.
Leontodon autumnalis, originally on the ground.
Leontodon hispidus, clothes, boot mud, or wind.
Lolium perenne, originally on the ground.
Luzula campestris, originally on the ground.
Lychnis alba, boot mud carried.
Nepeta hederacea, boot mud or by hedges?
Plantago lanceolata, originally on the ground.
Plantago major, originally on the ground.
Poa annua, originally on the ground.
Poa pratensis, originally on the ground.
Poa trivialis, f. *nemorosa*, boot mud carried always, I believe.
Potentilla anserina, boot mud carried always, I believe.
Potentilla reptans, boot mud carried always, I believe.
Primula veris, originally on the ground. The hybrid *P. veris* × *vulgaris* has never been taken in this covert. It has been found, and is growing this season (1917) at Pepperdale Fox Covert, in this parish, hybridized from *Primula vulgaris* v. *caulescens* in a farmhouse garden close by.
Prunella vulgaris, originally on the ground.
Ranunculus acris, originally on the ground.
Ranunculus bulbosus, originally on the ground.

Ranunculus repens, originally on the ground.

Rosa arvensis, hedges, but birds more commonly.

Rosa canina, hedges, but birds more commonly.

Rubus fruticosus, hedges and birds.

Rumex acetosa, originally on the ground.

Sambucus nigra, starling sown, always and everywhere.

Spiraea ulmaria, originally on the soil or more likely boot mud carried.

Stachys sylvatica, both by boot mud and by the hedges.

Stellaria graminea, originally on the ground.

Stellaria media, from cultivation, by boot mud.

Tamus communis, birds, especially blackbirds, but starlings too.

Taraxacum vulgare, wind and boots both wet and muddy. As good as gone at times, but always returning.

Trifolium pratense, originally on the ground.

Trifolium repens, originally on the ground.

Trisetum flavescens, originally on the ground.

Ulex europaeus, originally on the ground.

Urtica dioica, originally there or came at the planting in boot mud.

Veronica agrestis, from cultivation, on boots.

Veronica chamaedrys, originally on the soil.

Vicia cracca, boot mud, and by hedges, but not by the latter now.

Viola odorata, carpets the open parts of the covert after underwood clearings, came along the hedges.

Viola Riviniana, the same, but over much smaller areas. It can endure more shade too, a true hedge species.

In regard to this list of species, it may be safely assumed that if not actually on the spot where the covert now stands, which many of them were, all reached it at an early date in its existence as a woodland. *Acer*, *Anthriscus*, *Arum*, *Bryonia*, and the other well-known hedge-side species, would hardly be on the spot, as this covert was planted before the enclosure of the parish, i.e., when there was not then a field-hedge near it. On the other hand, as the existing fences followed almost at once, at the present date—quite 100 years after the event—we cannot disentangle the mixed skein of facts surrounding the advent of each species, for now no less than seven field-fences reach the covert's ringing-fence.

Here I should like to make a short digression as a student of soils and means of dispersal. It will be the greatest mistake in the huge plantings, which must follow this war, if the opportunity is not taken of finally settling the approximate history of the advent of species to isolated woods. The points for special observation are:

- (a) What is on the ground the new wood is to occupy.
- (b) What in the ringing fence surrounding it.
- (c) What in the hedges running up to this ringing fence.

(d) What species arrive annually from the year of planting till the final clearing.

(e) What are the opportunities for change.

(f) What are the means of carriage illustrated.

Finally, the Board of Forestry should have a travelling specialist to note these things as he goes about, but more especially to give advice freely to owners as to the species to be used for the main crop and the initial shelter, or much money will be wasted.

VII. NOTABLE SPECIES

The following species have been carried to Poolthorn Covert by some means. They may (1) either have been brought when it was originally planted, or (2) they may have arrived by carriage of some kind since that date, yet before 1891, when I first began to make full notes. They are of two classes, (a) those from the immediate neighbourhood; and (b) those from a greater distance.

(a) *Species from the immediate neighbourhood*

Ajuga reptans, mud carried.

Cnicus palustris, and its form with dense white hairs. Wind carried.

Conium maculatum, wind and mud carried.

Juncus conglomeratus, duck and mud carried.

Mentha verticillata, mud carried.

Orchis maculata, generally wind carried, more rarely clothes and mud carried.

Prunus domestica, on Very Chalky Boulder Clay only. Man, or blackbird or perhaps jay sown. Gone now, both in the covert and hedges near. Why?¹

Ribes grossularia, blackbird sown from the farm garden a quarter of a mile away. It is very common right in the covert in the more open parts on both soils. In masses 25 feet long by 15 wide at times.

Ribes rubrum, v. *sativum*, the same, but not so commonly found and never in masses.

Sonchus asper, by wind drift.

(b) *Species from a greater distance*

Circaea lutetiana, clothes carried to and from this covert every season.

Epilobium montanum, wind sown.

¹ I have gathered the fruit and carried it home to be cooked; but there has not been a bush left for ten years in the hedge on the Kimeridge Clay below the covert, or on the Very Chalky Boulder Clay within, yet the bushes were never cut out or dug up. In the next parish, North Kelsey, both the purple and yellow fruited forms are still found in the hedges, and this species is common enough in the hedges within a hundred yards of the table on which I write; but though they often flower, these low cut bushes have never fruited in twenty-eight years. I have proof that *P. domestica* is sown by men, sheep and birds; and that like *Pyrus malus* it was originally of garden origin. Its varieties and forms, like those of that species, seem endless.

Listera ovata, generally wind carried; more rarely clothes and mud carried. It was clothes carried by me from this covert for a time to the damp roadside one field to the north, where it survived for some ten years. It is only found on the Kimeridge Clay of the old central ride, now failing from over-shading. It can stand as much over-shadowing as *Arctium minus*.

Ranunculus auricomus f. *depauperata*, only on Very Chalky Boulder Clay. Mud carried.

Rumex nemorosus is found especially under *Quercus* shade. There were four species on my stockings when I left this covert, 5 September, 1892, *Circaea*, *Geum urbanum*, *Agrimonia* and this *Rumex*. A few of the last named were sticking to the stockings directly, far more often to the seeds of *Circaea* already securely hung there. The seeds of *Carex sylvatica* are carried by means of *Circaea* in the same way.

Viburnum Opulus, only on Very Chalky Boulder Clay. Blackbird sown.

VIII. FLOATING POPULATION

The species, which are uncertain, or have come to go and come again, perhaps more than once, are the following. They are boot mud carried for the most part.

Alchemilla arvensis, rarely there.

Anagallis arvensis, very rarely there.

Anthemis Cotula, generally there.

Arctium minus, there, gone, and back again, several times. It is clothes, bird and mammal carried, too. Generally there.

Atriplex patula, often there.

Bartsia Odontites, rarely there, but there now, 1917.

Brassica arvensis, generally there.

Bursa pastoris, generally there.

Chenopodium album, often there, but not now, 1917.

Chrysanthemum Leucanthemum, rarely there. Only a few plants left now, 1917.

Convolvulus arvensis, generally there somewhere.

Cynosurus cristatus, it is wind sown, too. It only comes and goes, for it hates shade of any kind.

Euphorbia exigua.

Euphorbia Helioscopia.

Euphorbia Peplus.

Mud carried from the carrs below on the south.

Festuca elatior, gone now from the Very Chalky Boulder Clay, I believe, on account of early ride mowing.

Filago germanica, carried on damp boots, or blown more often, from seed fields.

Galeopsis speciosa, from the carrs. Very rarely there.

Galeopsis Tetrahit, the same, but more often there.

Lamium decipiens, the same.

Leontodon nudicaulis, very rarely there. From the new grass pastures. Wind blown, or damp boot carried.

Matricaria inodora, from the tilth. Often there.

Myosotis arvensis, almost every season from the tilth, boot mud and clothes carried. In masses this season, 1918.

Papaver Rhoeas, rarely there.

Polygonum aviculare, often there.

Polygonum Hydropiper, in the central ride. Now gone. By over-shading I suppose.

Polygonum Persicaria, often there from the tilth.

Ranunculus arvensis, the same.

Rhinanthus Crista-galli, from the meadow next below.

Sagina procumbens, often there in a damp over-shaded spot. Mud carried.

Scrophularia aquatica, in the same spot as the above. Gone and back again more than once apparently.

Senecio vulgaris, gone and back several times.

Viola arvensis, the same.

IX. VERY CASUAL POPULATION

The following wind-sown species are more or less uncertain—common in masses at times, and then vanishing when the ground is fully occupied.

Carduus crispus, wind and boot mud carriage.

Cnicus arvensis, wind and boot mud carriage.

Cnicus lanceolatus, wind and boot mud carriage.

Cnicus palustris, wind and boot mud carriage.

All these thistles are present just now.

Conium maculatum, mud carried too.

Dipsacus fullonum, gone, but only a field away on the north.

Epilobium angustifolium.

Epilobium hirsutum, both much in evidence just now.

Lastrea Filix-mas, one plant only left, with fertile fronds, 1917¹.

Phleum pratense, very erratic. Now only by the S.W. hunting gate, wind or mud carried.

¹ In ninety-nine per cent. of cases *Lastrea* is purely wind carried, yet I do not doubt from the position of the first specimen discovered that this species arrived at Poolthorn by boot-carriage. Its single fertile offspring now in the Blackthorn Ride is absolutely sheltered from the south-westerly gales, but not from the north winds which rush down this ride. So young plants which have never spored may be found in the dense covert to the south-west of this plant, but nowhere else on the recently cleared ground, 1918.

X. SPECIES DUCK-CARRIED TO A POND

Some plants have been duck carried very many years ago to a shallow pond within the covert. It is now of no depth, and always dry in summer, and fully over-shaded, with a fifty-year old oak tree growing in its centre. The following are on the point of going:

Agrostis palustris, f. *nemorosus*.

Cardamine pratensis. It can never flower in the shade, and only survives by leaf-developed young plants. This gift was acquired to counteract defective seed development from late spring frosts, and not for shade growth, I believe; but if you want specimens for an herbarium, visit an over-shaded pond in August¹.

Carex elata, it never flowers now, but grows well.

Deschampsia caespitosa, wind and mud sown too.

Juncus conglomeratus, hardly ever flowers.

Juncus effusus, the same.

Juncus sylvaticus, the same.

The following have disappeared: *Angelica sylvestris*, *Callitriche stagnalis*, *Carex vulpina*, *Glyceria fluitans*, *Lemna minor*, *Ranunculus Drouetii*, *Veronica Beccabunga*.

XI. SPECIES OF SPECIAL INTEREST

The following species I put into a list by themselves, for they have been noted with especial interest.

Anemone nemorosa. This species arrived in 1892 by clothes carriage, I believe. It was before the starlings visited this covert, or I should have said that it had been carried by them, for it has come to Cadney Old Churchyard and elsewhere as I have observed by starling carriage. It was not by the then footpath track side, just off it—as plants from clothes-carried seeds generally are. There was only one seedling plant on Very Chalky Boulder Clay, in 1892. Now there is a big patch in the north end of the middle ride, but still only there as yet in this covert to my knowledge.

Centaureum umbellatum was introduced in 1900 by foot mud carriage as inferred from its situation. It extended vastly for three years, and then disappeared, and was no longer found till this season—1917—when it came by the same means as inferred from position.

Cerastium viscosum. By situation once appeared as a mud or wet boot carried species too. It spread rapidly for a time in the north side on Very Chalky Boulder Clay, but when the hedge grew up it also departed.

Daphne Laureola. I have been watching for the arrival of this species for over twenty years. There are eighty blackbird sown bushes in hedges half-a-

¹ Since the cutting down this spring (1918) one plant has flowered for the first time in eighteen years. A dozen or more plants are present. See *Journal of Botany*, 1917, p. 350.

mile to the east on Very Chalky Boulder Clay. It was introduced into this parish by the late Captain J. H. Skipworth, of the Chestnuts, Howsham, in 1843. The original bush was still alive when I came here in 1891, but has now gone. The curious thing is that only one plant has ever been detected to the north of the road past the Chestnuts. In the spring of 1917 at last, I found one plant on Kimeridge Clay in the south fence of the covert. It has always been sown by blackbirds, not the other Turdi, here and elsewhere where I have studied its dispersal in this county.

Fragaria vesca. Arrived after the starlings reached the covert. It is now found all round about the Blackthorns; but is as yet confined to one spot only in the S. ringing-ride of the old covert, though no doubt it will be bird sown or boot carried to other parts later. At first it was just under the edge of the Blackthorns, where no man could possibly stand.

Hypericum acutum. This species is also a new comer to the ride between the Blackthorns and the old covert. It too may have been starling carried; but from the position of the plant first found I judged boot mud carried from the roadside north of the covert.

Lactuca virosa. This is one of my typical cases for clothes carriage. On 21 October, 1901, I was at a covert shoot at Poolthorn as a spectator. One of the guns told me that he had been at a shoot on the meals (i.e., our maritime sand dunes), and that his legs and his clothes were covered with seeds. I got one—the only one I could find—on his coat and named the species he was referring to from it. On the 28 August, 1903, mark the dates, I found one plant only—but a very fine one—of *Lactuca virosa* in the south-western corner of the ringing-ride of Poolthorn Covert, just by the spot where I took a seed from my friend's coat. There can be no doubt that he sowed it there. I took a fragment of this plant as a typical specimen of clothes carriage for the County Museum; the rest of the plant was cut away later, before seeding time, in ride cleaning up for that year's shootings. It has never been seen before or since. If that is not a perfectly typical case of clothes carriage, where shall I get one? I have the original seed taken in the County Collection, as well as the part of a plant grown from another two years later.

Lonicera Periclymenum. There is one bird-sown bush at the S. end of the central ride. It has never flowered since I have known this covert. Blackbird sown.

Lotus tenuis. This appeared in the ringing-ride at the south-eastern corner, at a spot where a shooter is generally placed. It was evidently, from its position close by the footpath, boot mud carried. It was there for two seasons only five plants in all.

Orchis pyramidalis. Was in the north ringing-ride on Very Chalky Boulder Clay in 1891 when I first visited the covert. It died out under the high hedge growth which was allowed for some years. After the hedge was kept low it was again in evidence after three seasons, for about six. Then it disappeared;

but for what reason I cannot judge. It has not been seen for some years now either there or elsewhere in this parish on the Very Chalky Boulder Clay outcrop from which it was wind sown into the covert. These facts are curious. Perhaps they have to do with early meadowing of the rides and road sides?

Picris echinoides. When I came here in 1891, this species was in quantity on the south ringing-ride of the old covert, on Kimeridge Clay. This fence was allowed to grow up, and was then cut down. The hedger who did this work carried this species on his boots or clothes to two other hedge sides to which he went immediately to work. Early ride mowing has destroyed it eighteen years ago in its original place in the covert, though in 1914 it was still in the corner of a pasture just outside the ringing-ride fence. As these are the only instances of this species in this wide parish, I believe that it was originally carried here on a shooter's clothing or boots. It is not found in any of these places now.

Plantago media. After the cutting down of the northern ringing fence, this species was seen for a few years on the Very Chalky Boulder Clay. At first by boot carriage by the footpath side; later slightly nearer the fence. It has now gone apparently, but why I cannot say. Can it be meadowed out of existence? It is found elsewhere in this parish, but only on the Very Chalky Boulder Clay as in this covert, more rarely still on Very Chalky Sandy Glacial Gravel.

Rhamnus catharticus. There is one staminiferous bush on the Kimeridge Clay, which was sown there by a blackbird dropping during the great frost of 1895. I found in the long frosts of 1895, 1916 and 1917 that these birds never turn for food to the berries of this species till the late spring when all other fruits are exhausted.

Rubus Idaeus. One root only, I believe blackbird carried, in the Blackthorn Ride. It may have been starling carried, but blackbirds are its usual transporters. It is the wild form, not that of our gardens.

Scilla non-scripta. This species appeared on the edge of the Blackthorns in 1911. There was only one plant at first. It is now, 1917, spreading rapidly. There can be little doubt that it was starling carried to the spot where I first saw it. It is sometimes mud carried too, I know; and no doubt is extending its range at present by this means in the covert. That was, however, not the means by which it first arrived, if the first plant's situation is a true clue in any case. No shooter could have stood under the fetid blackthorn bushes where I found it.

Senecio erucifolius. There are two plants of this species on the Kimeridge Clay in the W. ringing-ride this season, 1917. By position they have been carried on wet boots rather than by wind, for this species grows on the road side on Very Chalky Boulder Clay one field to the north in a stream valley, which has cut through the upper strata of the Chalky Boulder Clay to its basement or Very Chalky Boulder Clay bed.

XII. CONCLUSION

What has been learned by the labour of twenty-six years on this covert, which is now 120 years old, when it is compared with other coverts and woodlands round, is as follows:

(1) The soil a woodland grows on is a most important consideration both as regards (a) the future main crop and (b) the nursing species.

(2) That the species used in planting should be most carefully selected in regard to these two matters. These are the most important observations.

(3) That the sheltering species should be wholly removed, and not left to take up valuable room after doing their work, as is so often the case.

(4) That in time most, if not all, woodland species adapted to any particular soil or soils gradually arrive, by chance means, at a covert even as isolated as Poolthorn is.

(5) The modes of carriage are as various as the visitors to a covert are frequent or rare.

(6) Unless it is an old woodland soil, i.e., has practically all the species that it is capable of growing, a covert is always receiving fresh, though perhaps only temporary, additions to its flora.

(7) Even when a covert has practically every species that it can grow, some are ever ebbing or flowing, here for a few seasons in masses, and then as good as gone or absent, as the circumstances of chance or seasons reduce rapid fluctuations and changes, or cause them to increase.

(8) Man is the all-potent influence in British woodlands, but unassisted nature—thanks to chance, gales, fungus and insect pests—is a good second in causing those local disturbances which bring about successive changes.

(9) It would appear that species often arrive at woods which are newly planted at a date before the soil is fitted for them as true woodland species. This seems to be the case with *Anemone nemorosa* at Poolthorn, though the soil seems quite in right condition for *Scilla non-scripta*. It may be that *Anemone* dropped on the wrong spot, rather too far out in the ride in this soil new to woodland. On the other hand *Rubus Idaeus* is too over-shaded where the seed has been dropped. *Centaureum* has not met with its right soil, while *Fragaria* is just at home. *Lotus tenuis* was never at home; neither is *Lonicera* where the seed was dropped.

(10) The evidence I possess concerning this covert and other woods, seems to point to the conclusion that seeds are ever arriving from near at hand or more distant localities, but they rarely happen on the circumstances that they exactly require, and so in the greater number of cases perish at an early date in their existence as plants.

CRYPTOGAMIC VEGETATION OF THE SAND-DUNES OF THE WEST COAST OF ENGLAND¹

By W. WATSON

(With three Figures in the Text)

In the sand-dune formation bryophytes and lichens are so prominent that any attempt to deal with its ecology is very conspicuously incomplete unless this vegetation be taken into account. The bryophytes and lichens are not only important in forming humus and so preparing the ground for the higher plants, but they are characteristic and sometimes dominant partners in the different associations belonging to the formation. The purpose of this paper is to give some account of the non-vascular plants characteristic of sand-dunes, and the phanerogamic constituents of the various associations will only be introduced where it is necessary to enable the reader to gain a comprehensive view of the associated plants and to correlate these results with those of previous workers (3, 4, 5, 6, 10).

My investigations have been carried on for many years and on a great length of coast-line, extending from Bude in Cornwall to Seascale in Cumberland. The dunes occurring within this area have many features in common, so that only those at Braunton in Devon and Burnham in Somerset will be dealt with in detail. The dunes of Lancashire are the most extensive ones on our coasts, but their natural characters have been somewhat interfered with during recent years by drainage and planting, and though their *Brya* and *Harpidia* associations are superior to those of any other dunes in this country, they are very poor in lichens and are in some respects less natural than those of N. Devon.

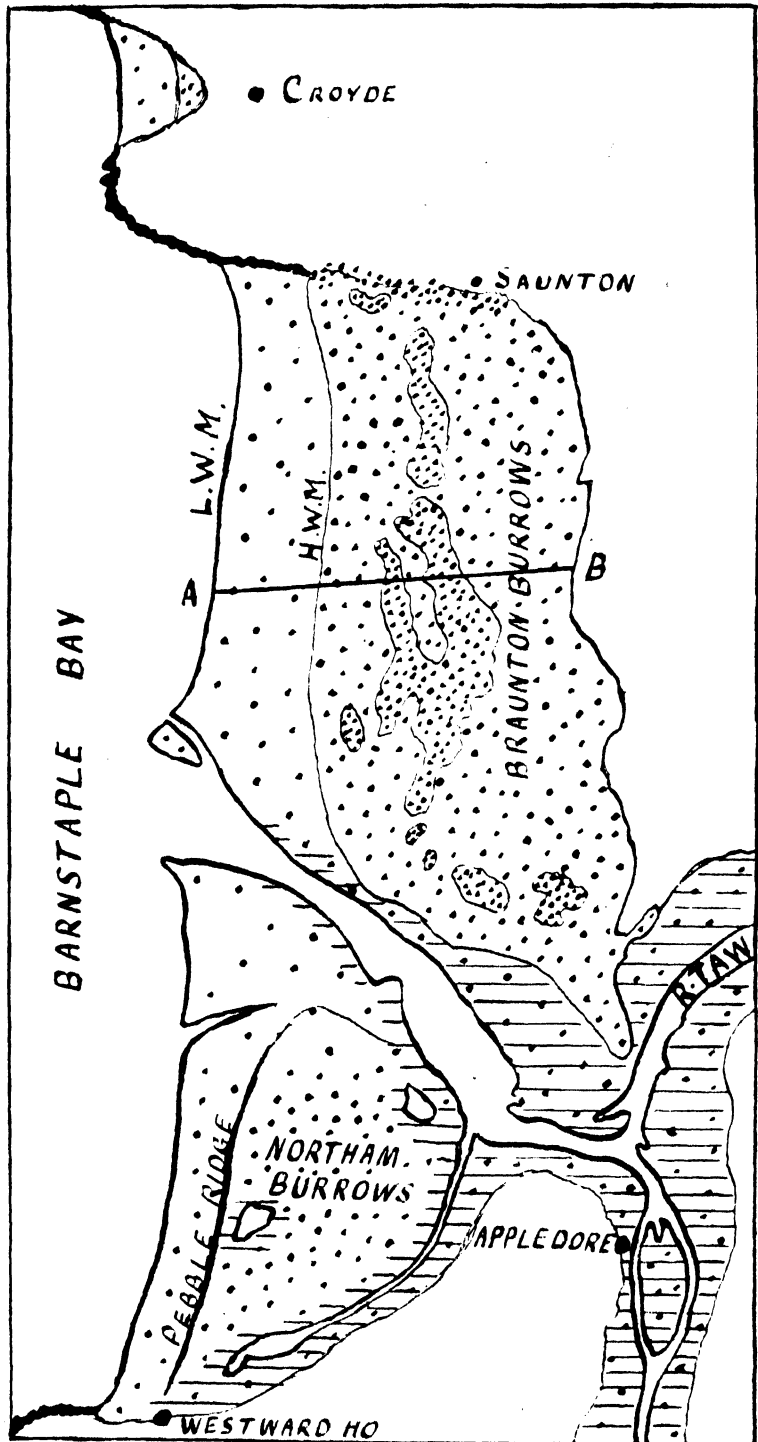
THE "BRAUNTON BURROWS"

The sand-dunes of Braunton, known as the "Braunton Burrows," are about 3 miles long by $1\frac{1}{2}$ miles wide, and are situated in North Devon, facing west towards Barnstaple or Bideford Bay (see Map, Fig. 1). At their southern boundary they are limited by the estuary of the Taw, but smaller dunes occur on the southern side of the river, and near Westward Ho an interesting pebble ridge is formed, this being prevented from encroaching on the golf-links by the labours of the inhabitants of the district. The eastern boundary lying towards Barnstaple abuts on marshy land. This portion is used by the golfers,

¹ Part of a thesis accepted for the degree of D.Sc. at the University of London.

some drainage and levelling has taken place, and it is evident that its natural characters will be seriously interfered with during the coming years. On the northern side is Croyde Point, a headland of Devonian slates and sandstones

FIG. 1.
SKETCH-MAP OF
BRAUNTON BURROWS
AND NEIGHBOUR-
HOOD. Scale 1 inch
to a mile. 1 : 63,360.
The sand-covered
area is dotted: the
increase in height of
the sand-hills is re-
presented by increas-
ing closeness of the
dots. The highest
sand-hills exceed
50 feet and in some
cases 100 feet. Where
mud or muddy sand
(sometimes forming
salt-marsh) borders
the rivers horizontal
lines are added.
Rocky headlands are
indicated by thick
wavy lines. Water
and cultivated land
are left blank. The
line *AB* represents
the line of section
of Fig. 2.



which only interrupts the dunes, miniature "burrows" being found in the bay between this headland and the more northerly Baggy Point. Northward again (out of the map) we get a wide stretch of sand and a narrow belt of dunes, which have been very much changed to form the 18-hole Woolacombe golf-course.

The southern parts of the dunes are slightly screened from the full force of the prevailing south-western winds by the high coast-line from Clovelly to Hartland Point, so that the best-developed dunes are towards the north. The northern portion is the most interesting area and is the part to which most of my remarks refer.

Topographical Divisions and Vegetation of the Burrows

The Burrows and their limiting portions may be topographically divided as follows (see Figs 1 and 2).

1. *Flat Sands*. On the seaward side there is a stretch of sand (Saunton Sands) which is over $\frac{1}{2}$ mile wide at low tide, and is practically bare of vegetation. An occasional tuft of *Salsola* may be met with, but the halophytic association of strand-plants found on the seaward sides of some sand-dunes is absent.

2. *Scattered and comparatively small fore-dunes*. The flat sands are succeeded by a number of small sand-hills ranging in height from a few feet to as much as 15 feet. They are more or less linked up to form a sand-cliff

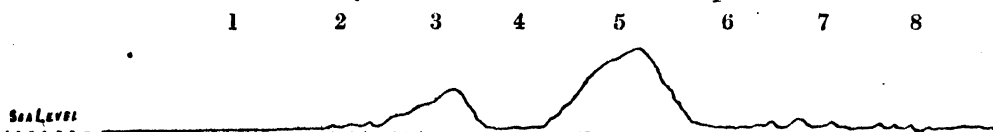


FIG. 2. SECTION ACROSS BRAUNTON BURROWS (line AB in Fig. 1). Horizontal scale 1 : 30,000 or about 2.1 inches to 1 mile. Vertical scale about 10 times horizontal scale.

Topographical regions: 1. Flat sand covered at high tides. 2. Fore-dunes (scattered and small very mobile sand-hills). 3. Very mobile dunes rising to 50 feet. 4. Brackish "slacks" (zone of *Riccia crystallina*). 5. Mobile sand-hills rising to 100 feet. 6. The second line of slacks, usually with *Harpidia*. 7. More or less stable sand-hills. 8. Flats with scattered stable sand-hills.

parallel to the sea, but the appearance of this cliff is constantly changing, "wash-outs" and "blow-outs" being common. Practically the only vegetation present on them is *Ammophila*, though a little *Salsola* or *Crithmum* may occasionally be met with on the face of the cliff, and a slight tendency towards an association of strand-plants may sometimes be detected in the larger inlets of the cliff. The *Agropyretum juncei* association which is shown on some parts of the Somerset, Cornish, Lancashire and Cumbrian (Seascale) coasts is absent, and no non-vascular plants were noticed on these ever-changing dunes.

3. *Large Sand-hills*. These form an almost continuous ridge more or less parallel to the sea, with a tendency towards a position at right-angles to the incident and prevalent south-western winds. The hills are sometimes over

50 feet high, the sand is very mobile, and the dominance of *Ammophila* is very pronounced, this plant often being the only one met with. *Viola canina*, *Erodium cicutarium*, *Potentilla anserina*, *Sedum acre*, *Senecio jacobaea*, *Leontodon hispidum*, *Anagallis arvensis*, *Cynoglossum officinale*, *Nepeta glechoma*, *Teucrium scorodonia*, *Euphorbia paralias*, are occasionally met with. No bryophytes or lichens are present except on the inner edge, but a few Agarics sometimes occur. The unstable character of these hills and their deficiency in humus render it difficult for slow-growing plants to establish themselves. Fungal mycelium is sometimes abundant but it is only when the conditions are sufficiently stable that conidiophores are developed. This development, despite its rapidity, is only occasional, so that it is not surprising that comparatively slow-growing mosses are unable to find a footing.

4. *Line of slacks. Zone of Riccia crystallina.* The ridge of sand-hills is usually succeeded by a line of wide furrows or "slacks" which run in a direction more or less parallel with the edge of the sea. They are sometimes interrupted here and there by small sandhills with the characteristic Marram grass (*Ammophila*), but are often level and unbroken for hundreds of square yards. During wet weather or high tides small lakes are formed in them but they may be fairly dry both in summer and winter. The presence of these small lakes was a common occurrence during the winter months, but during recent years the work of drainage, carried on for the preservation of the more inland golf links, has limited and in some places entirely prevented their formation. Very little grows on these slacks, the light brown colour of the sand being almost unrelieved by any tint of vegetation. The most prominent interruptions are formed in moist places by greenish patches of *Vaucheria* (*V. sessilis*, *V. dichotoma*), pale green rosettes of a liverwort (*Riccia crystallina*) and patches of *Glaux maritima*, whilst drifted matter such as seaweed is scattered anywhere. A dark looking incrustation on the sand is sometimes caused by a small form of *Collema pulposum*, but more usually by the allied *C. glaucescens*, whilst a whitish efflorescence may be due to the presence of *Arthopyrenia areniseda*. On their outer edges mosses appear, *Bryum argenteum* being the one met with nearest to the sea, occurring on small sand-hills amongst *Ammophila*, whilst small sand-islands (1 to 2 feet high) yield *B. pendulum* associated with Marram grass and *Plantago coronopus* var. *pygmaea*. Other plants occurring on the flats are *Samolus valerandi*, *Sagina apetala* var. *prostrata*, *Arenaria peploides*, *Chenopodium rubrum*, *Barbula tophacea*, *Aneura pinguis*, and the small Discomycete *Barlaea crouani*.

Some of the slacks which are less liable to flooding have a much more prolific vegetation and approach in vegetational character those found further inland. The absence or rarity of bryophytes and lichens in this zone is partly to be explained by the occasional flooding with brackish water, of which few mosses have any tolerance, but is largely due to the mobile nature of the substratum, the bryophytes and lichens which occur being able to do so owing to

the protective influence of other vegetation in preventing them from being covered by sand, or owing to the occurrence of moist areas in which the sand is more firmly held together by the greater weight and the capillary attraction of the water-film between the particles. The fact that *Bryum argenteum* is the first moss to be met with is significant because it is a moss which spores freely and has a xerophytic device in the non-chlorophyllous apices of its leaves which cover over the transpiring portions; but any moss with similar advantages could take its place. The moss met with nearest to the sea depends largely on local circumstances, but *B. argenteum*, because of its high frequency, wide distribution and economic advantages is one of the first mosses to occur in bared places. The other Brya have similar though less pronounced advantages. *Riccia crystallina* is well adapted to its moist substratum; its young thalli (developed from the spores) find fixing points in the moist sand, expand quickly, and form small rosettes over which the sand grains are carried, while the numerous air chambers provide it with sufficient air when it is submerged.

5. *The second group of sand-hills.* These are parallel with the first ridge but are more uneven, their general parallelism to the sea being often obscured by flanges running at various angles from them. The general height of this inconstant ridge is over 50 feet and the highest peaks may sometimes reach 100 feet. The sand on the outer portions of this ridge is continually shifting, but on the landward side the sand is less mobile and the dunes are more constant in form. *Ammophila* is the only plant which is a constant constituent of the ridge, and on the outer shifting sand is often the only plant present. The same species of flowering plants which occur on the first group of sand-hills are also found here, and in the less mobile portions *Viola curtisii*, *Galium verum*, *Erigeron acre*, *Carlina vulgaris*, *Cnicus lanceolatus*, *Sonchus oleraceus*, *Scrophularia nodosa* and *Ajuga reptans* are also met with. The bryophytes become more conspicuous, *Tortula ruraliformis* and *Camptothecium lutescens* (sand-hill form) being the dominant species, whilst other abundant species are *Trichostomum flavovirens*, *T. crispulum*, *Ceratodon purpureus*, and *Bryum pendulum*. *Tortula ruralis*, and intermediates with the closely allied *T. ruraliformis* are not infrequent; *Bryum argenteum* is frequent, and *B. caespiticium* is occasionally found. Lichens are fairly abundant but consist of few species, the foliaceous Peltigerae (*P. rufescens*, *P. canina*, *P. spuria*) and the gelatinous *Collema crispum* being practically the only species represented.

All these lichens have a spreading habit, forming on the surface of the sand leaf-like expansions over which the mobile sand-grains readily pass. The algal symbiont is a cyanophyceous one, and in *Collema* there is a large amount of mucilage, which functions as a water reserve. The dominant mosses have xerophytic devices. *Tortula ruraliformis* has plicated leaves with recurved margins and hyaline apices. It is often embedded in the sand, and during dry weather the leaves are appressed to the stem and somewhat twisted, so that only the hyaline apices are exposed. *Camptothecium lutescens* has deeply

plicate leaves with recurved margins. It has not so restricted a habitat as *Tortula ruraliformis*, since it is not uncommon on dry soil in calcareous districts, whereas *T. ruraliformis* is seldom found except on sea sand. *Trichostomum flavovirens* is one of the few mosses which is tolerant of haloid salts. All three of these mosses are chiefly dependent on vegetative means for their reproduction.

6. *The second line of slacks.* These are even less definite in position and form than the first line of slacks, and are often split up into smaller portions by offshoots from the second ridge of sand dunes. Their topographical relations are more constant owing to the sand being less mobile, but the water supply is very variable; a few of the hollows form permanent pools, some have a covering of water for a large portion of the year, whilst a large number are only occasionally flooded. This variability of water-supply, together with the drainage work now carried on, is responsible for a curious intermixture of plants, and some of the slacks must be considered to be in a transitory stage between the state of almost permanent pools and the drier state which will eventually ensue through drainage. In the wetter slacks the dominant plant is often one of the Harpidia group of mosses—*Hypnum aduncum* var. *pseudosendtneri*—but it is often hidden by *Eleocharis palustris* and *Hydrocotyle vulgaris*, which then appear to form the dominant members of the association. The Shoreweed (*Littorella lacustris*) is sometimes extremely abundant, forming almost pure patches scores of square yards in extent. Other frequent plants are *Arenaria peploides*, *Glauz maritima*, *Anagallis tenella*, *Samolus valerandi*, *Blackstonia perfoliata*, *Mentha aquatica*, *Chenopodium rubrum*, *Hypnum cuspidatum*, whilst the rosettes of *Riccia crystallina* again form a prominent feature on the borders. Algae are very abundant but were not particularly investigated, the most prominent being *Chara fragilis*, *Vaucheria sessilis*, and *Mougeotia recurva*. Some of the small algae noticed include *Tribonema bombycina*, *Dictyosphaerium ehrenbergianum*, *Tetracoccus botryoides*, *Scenedesmus obliquus* (com.), *S. quadratus*, *Oocystis elliptica*, *Selenastrum gracile*, *Pandorina morum*, and species of *Chroococcus*, *Anabaena*, *Oscillatoria*, *Gloeocapsa*, *Pediastrum*, Desmids (*Mesotaenium* and *Cosmarium* spp. are abundant) and Diatoms (*Amphora ovalis*, *Epithema*, and species of *Navicula*, especially *N. viridis*, are abundant). The slacks of a less wet character are more or less grassy and have a more varied flora. The presence and occasional abundance of the plants found in the wetter slacks indicate the changes which are occurring through drainage, changes which are also denoted by the intermixture of the following plants: *Cerastium vulgatum* f, *Sagina nodosa* f, *S. procumbens* f, *Potentilla anserina* f, *Leontodon nudicaule* o, *Centaureum vulgare* f, *C. pulchellum* o, *Gentiana amarella* o, *Euphrasia officinalis* o, *Prunella vulgaris* o, *Rumex crispus* var. *trigranulatus*, *Juncus bufonius* and var. *fasciculatus* a, *Carex arenaria* o, *Hypnum cuspidatum* f, *H. stellatum* f, *H. aduncum* and form *falcatum* f, *Bryum pseudotriquetrum* and var. *compactum* f, *B. argenteum* o,

B. pallens o, *Trichostomum flavovirens* o, *T. crispulum* o, *Ceratodon purpureus* f, *Pellia fabbrioniana* f, *Aneura major* (sand-dune form) f, *A. pinguis* f, *A. incurvata* o, *Petalophyllum ralfsii* f, *Lophozia badensis* f, *Moerckia flotowiana* o, *Hygrophorus conicus* f, *H. pratensis* f, *Sphaerospora asperior* f, *Aphanocapsa grevilleana*, *Nostoc vulgare* f, *Aphanotheca microscopica* f. A peculiar form of *Barbula tophacea* with leaves distinctly decurrent is also frequent (Fig. 3); the extension of the leaf bases seems to be related to the intermittent supply of water. Incrustations similar to those of *Arthopyrenia areniseda* were noticed but as no perithecia were found it is unsafe to include the plant. *Teucrium scordium*, *Scirpus holoschoenus*, *Juncus acutus* and *J. maritimus* are also present and sometimes abundantly so, but they are not widely distributed. Cyanophyceous algae (Myxophyceae) are very abundant, their relative preponderance over other small algae being due to their more copious gelatinous investments rather than to any action of the colour. It is also significant that the lichens present on the outer dunes belong to genera which have a blue-green algal symbiont.

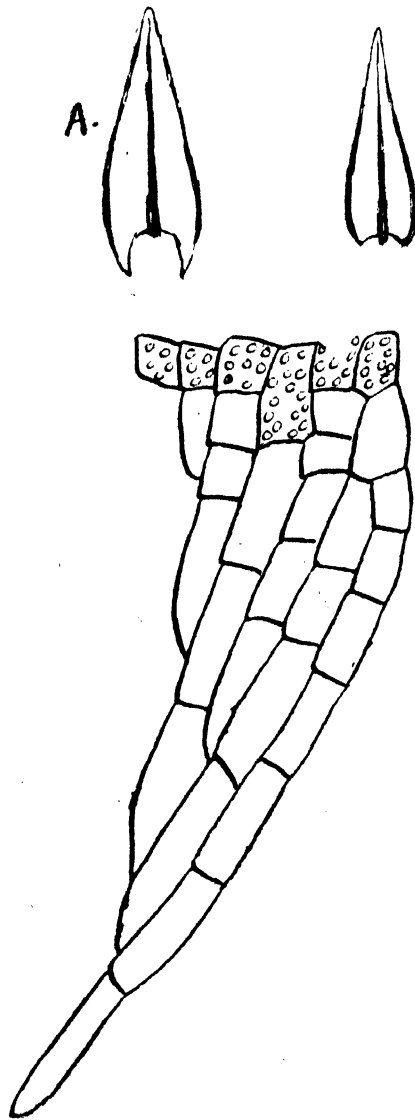


FIG. 3. *BARBULA TOPHACEA*, MITT.

- A. Leaf of form from Branton Burrows, $\times 15$, showing auricles. An auricle is shown below, $\times 350$; the upper cells are chlorophyllous, the lower are hyaline.
B. Leaf of type, $\times 15$. Auricles are absent or poorly represented.

cium lutescens, *Peltigera canina*, *P. rufescens*, or *Cladonia furcata*. A careful scrutiny of an area of about 20 square yards on one of these sand-hills yielded the following results: *Ammophila arenaria* d, *Ranunculus bulbosus* o,

7. *More or less stable sand-hills*. These are in various stages of transition between mobile and fixed dune and form much lower eminences than the former. Most of the plants given in *Types of British Vegetation* as belonging to the fixed dune association are met with, together with some plants of the *Ammophiletum arenariae*. Bryophytes and lichens become more abundant, *Tortula ruraliformis* often being the dominant plant, though its supremacy may be disputed by *Camptothecium*.

Erophila verna f, *Viola canina* o, *Cerastium semidecandrum* o, *Arenaria serpyllifolia* a, *A. leptoclados* f, *Geranium molle* o, *Erodium cicutarium* f, *Potentilla anserina* o, *Sedum acre* f, *Filago germanica* o, *Hypochaeris radicata* o, *Senecio jacobaea* o, *Taraxacum erythrospermum* o, *Anagallis arvensis* f, *Centaureum umbellatum* o, *Myosotis collina* o, *Solanum dulcamara* (o in damper spots or in places shaded by higher sand-hills), *Scrophularia nodosa* o, *Veronica arvensis* var. *nana* o, *Teucrium scorodonia* f, *Plantago coronopus* var. *pygmaea* o, *Euphorbia paralias* f, *E. portlandica* o, *Carex arenaria* f, *Phleum arenarium* a, *Aira caryophyllea* o, *Poa compressa* (small form) o, *P. annua* o, *Tortula ruraliformis* (a and with capsules), *Camptothecium lutescens* a, *Bryum pendulum* o, *Collema crispum* o, *Leptogium scotinum* var. *sinuatum* o, *Bilimbia sabuletorum* o, *Biatorina coerulea-nigricans* o. The last-named lichen is covered with a floury substance (pruina) and this acts as a xerophytic device. Other plants not present in this particular area but occurring on similar and neighbouring sand-hills are *Reseda luteola* o, *Viola curtisii* f, *Hypericum hirsutum* o, *Ononis repens* f, *Potentilla reptans* o, *Oenothera biennis* o, *Erigeron acre* o, *Filago minima* r, *Achillea millefolium* o, *Carlina vulgaris* a, *Cnicus lanceolatus* o, *C. arvensis* o, *Cynoglossum officinale* f, *Lycopsis arvensis* o, *Myosotis versicolor* o, *Echium vulgare* f, *Solanum nigrum* o (usually in damper places), *Verbascum thapsus* o, *Sibthorpia europaea* (unexpectedly found in moist nooks), *Thymus serpyllum* a, *Iris foetidissima* f, *Tortula ruralis* o, *Ceratodon purpureus* f, *Barbula unguiculata* o, *B. convoluta* f, *B. tophacea* o, *B. gracilis* o, *B. fallax* o, *Trichostomum flavovirens* f, *T. crispulum* o, *Bryum capillare* o, *B. caespiticium* o, *B. pendulum* o, *Brachythecium albicans* o, *B. glaucescens* o, *Collema crispum* a, *C. cheileum* o, *C. ceranoides* o, *C. pulposum* o, *Leptogium lacerum* f, *L. tenuissimum* o, *Peltigera rufescens* a, *P. canina* a, *Usnea hirta* o, *Evernia prunastri* f, *Ramalina farinacea* o, *Urceolaria scruposa* f, *U. bryophila* o, *Squamaria crassa* o, *Cladonia furcata* a, sometimes d, *C. pyxidata* and var. *pocillum* f, *C. fimbriata* o, *C. cervicornis* o (= *C. subcervicornis* Wain.), *C. pungens* and form *foliosa* f, *Rhizocarpon petraccum* r (on small stones).

8. *Flats with scattered sand-hills.* The definition between the flats and hills gradually gets less marked as the latter become more stable, and they finally merge together into dune-pasture land. The sand-hills have a similar floristic composition to those of the previous division, though the characteristic dune plants become less marked and invasions of other plants such as *Hypnum cupressiforme* and var. *elatum*, and *Lophocolea bidentata*, occur. *Camptothecium lutescens* is often more abundant than *Tortula ruraliformis* and some of the smaller eminences are dominated by *Carex arenaria*. The accompanying dune-marsh association is similar to that of division 6. The most noticeable additions are *Cardamine pratensis*, *Lithospermum officinale*, *Orchis incarnata*, *Epipactis palustris*, *Juncus glaucus*, *J. effusus*, *Scirpus tabernaemontana*, *Pteris aquilina*, *Hypnum riparium*, *H. lycopodioides*

and *H. aduncum* var. *paternum*. Sedges are more abundant, the following species being noted: *Carex flacca*, *C. oederi*, *C. extensa*, *C. punctata*, *C. goode-novii*, *C. verna*, *C. hirta*, *C. pilulifera*.

Trees or shrubs are rare on any part of the dunes. *Salix repens* is present on the flats towards the south-east, but is rarely found on the sand-hills. A wind-swept elder or privet may be occasionally seen, and a small clump of sycamore trees stands out prominently on one of the small eminences. The lichens noticed on these trees were not distinct from those found on trees in more inland situations. The chief species found include *Usnea florida*, *U. hirta*, *Evernia prunastri*, *Ramalina fraxinea*, *R. calicaris*, *R. fastigiata*, *R. farinacea*, *R. pollinaria*, *Parmelia saxatilis*, *P. sulcata*, *P. revoluta*, *P. caperata*, *P. physodes*, *P. perlata*, *P. fuliginosa* var. *laeto-virens*, *Xanthoria parietina*, *Physcia tenella*, *P. ulothrix* var. *virella*, *P. pulverulenta*, *P. aiopolia* var. *cercidia*, *Lecanora rugosa*, *L. chlarona*, *Lecidea parasema* and its variety *elaeochroma*, *Buellia canescens*, *Rhizocarpum alboatrum* and *Opegrapha atra*.

The Associations on the Burrows

A. The Strand.

1. An association of strand plants is very poorly represented.

B. The Sand-hills.

2. A sea-couch-grass association (*Agropyretum juncei*) is absent.
3. A Marram-grass association (*Ammophiletum arenariae*) is well shown. There are at least three sub-associations represented. (a) On the seaward side the sand is mobile, the dominance of *Ammophila* is very pronounced, other phanerogamic plants are infrequent, and mosses or lichens are absent or very rare. (b) In the second the sand is less mobile and though *Ammophila* is still dominant, other phanerogamic plants, especially *Euphorbia paralias*, are frequent. The mosses, *Tortula ruraliformis* and *Camptothecium lutescens*, are very abundant, whilst the lichen *Peltigera canina* is conspicuous and common. (c) On the landward portion the dunes are fairly stable, the dominance of *Ammophila* is less pronounced and *Cladonias* (especially *C. furcata*) are often very abundant.

4. A fixed dune association is present on the landward side of the Burrows. *Ammophila arenaria* and *Carex arenaria*, the two plants chiefly concerned in the fixation of the dunes, become less abundant and finally disappear in the dune pasture. *Salix repens* plays a very small part in the fixation of these dunes, and the dry association of *Salix repens* ((6), p. 350) is unrepresented. The dunes which are almost stable are characterised by squamose and fruticulose lichens. *Urceolaria scruposa*, *U. bryophila* and *Cladonia pyxidata* var. *pocillum* are frequent and some fruticulose lichens (*Ramalina farinacea*, *Usnea hirta* and *Evernia prunastri*), which are usually found on trees, are characteristic members of this sub-association. "A grassland association of dune hollows" ((6), p. 351) occurs on the landward side. Like the almost stable

dunes it is an approach to fixed dune, and is probably better considered as a sub-association.

C. The slacks or hollows between the sand-hills.

5. A *Riccia crystallina* association is present on the outermost slacks to which sea-water has occasional access. *Glaux maritima* is the only phanerogamic plant common in this association and *Vaucheria dichotoma* is a frequent member.

6. The dune marsh association is well shown. The chief phanerogamic constituents are *Hydrocotyle vulgaris*, *Anagallis tenella*, *Eleocharis palustris* and *Littorella lacustris*, but the dominant plant is often a Hypnum belonging to the Harpidium group, so that this association may be styled a Harpidia association. Algae are abundant and chiefly belong to the Cyanophyceae. Another facies of this association is characterised by the dominance of *Juncus acutus*.

7. Dune pools are sometimes present, are usually more or less brackish, and contain little vegetation besides *Chara* and other algae.

8. In the damp hollows between the sand-hills bryophytes (especially *Bryum* spp.) are abundant, and this association may be called a Brya association. *Salix repens* is sometimes present and Carices are frequent (see "Damp Association of *Salix repens*" (6), p. 351).

D. Associations bounding the Burrows. On the landward side dune pasture is found, a shingle ridge occurs near Westward Ho, salt marsh is present on the shores of the Taw estuary, whilst salt marsh pasture is found on Branton Marsh.

THE SOMERSET SAND-DUNES

The only part of the Somerset coast which has well-marked sand-dunes lies between Burnham and Brean Down. They extend along the coast for over 5 miles and at their widest point are about half a mile broad. They are much inferior to those of Branton, not only in extent but also in the altitude of the sand-hills themselves. There are no well-marked lines of ridges and furrows, but numerous pools occur, most of which are of temporary duration.

In some parts the association of strand plants or the *Agropyron juncei* is present. The only mosses (*Tortula ruraliformis*, *Bryum intermedium*, *Trichostomum flavovirens*) noticed in these associations are also found further inland, but they may occur just above high-water mark, and *T. flavovirens* is more characteristic of these associations than of those further inland.

The dunes are of a less shifting nature than those of Branton, the belt in which the Marram grass is almost exclusive of other vegetation being a narrow one. The phanerogamic vegetation of the hills in which *Tortula ruraliformis* and *Camptothecium lutescens* are the dominant mosses is similar to that of Branton, the Marram grass being predominant, while *Carex arenaria*, *Sedum acre*, *Euphorbia paralias*, *Cynoglossum officinale* and *Erodium cicutarium* are

abundant, but there are local differences such as the absence or infrequency of *Viola curtisii*, *Teucrium scorodonia*, *Filago germanica*, *Centaureum vulgare*, *Euphorbia portlandica*, *Erigeron acre*, *Juncus acutus*, and the presence or more common occurrence of *Trifolium arvense*, *Oenothera ammophila*, *Carduus tenuiflorus*, and *Anthyllis vulneraria* (this is placed under var. *pulchella* Vis., *J. of Bot.* July, 1917).

The cryptogamic vegetation is also similar, as the following list shows: *Tortula ruraliformis* sd, *Camptothecium lutescens* (sd and in wet weather sometimes covered with *Symplocia muscorum*), *Tortula ruralis* o, *Ceratodon purpureus* a, *Barbula fallax* and var. *brevifolia* a, *B. tophacea* o, *Trichostomum flavovirens* o, *Bryum pendulum* o, *B. capillare* a, *Brachythecium rutabulum* o, *B. albicans* o, *Eurhynchium megapolitanum* o, *Amblystegium serpens* o, *Cladonia furcata* ld, *C. pyxidata* and var. *pocillum* f, *C. fimbriata* o, *C. cervicornis* (= *C. subcervicornis* Wain.) o, *C. pungens* f, *Pelligera canina* a, *P. rufescens* f, *P. polydactyla* f, *Collema pulposum* o, *C. crispum* o, *Leptogium scotinum* var. *sinuatum* f, *L. lacerum* f, *Urceolaria scruposa* o, *U. bryophila* o, *Bacidia muscorum* o, *Biatorina coeruleonigricans* o. On the dunes which have been rendered more stable by the planting of *Hippophaë rhamnoides* these are supplemented by *Hypnum cupressiforme* var. *ericetorum* a, *Eurhynchium confertum* f, and *Hylocomium squarrosum* a.

In the damp grassy sandy hollows an association of plants occurs with species of *Bryum* abundant, and this might fitly be called a Brya association. The most common plants are *Hydrocotyle vulgaris*, *Lycopus europaeus*, *Galium palustre*, *Sagina nodosa*, *Juncus bufonius*, *J. glaucus*, *Bryum warneum*, *B. pendulum*, *B. bimum*, *B. pseudotriquetrum*, *Brachythecium mildeanum*, *Barbula tophacea*, *Funaria hygrometrica*, *Hypnum polygamum*, *Pellia fabbroniana*, *Petalophyllum ralfsii*, *Aneura pinguis*, *A. incurvata*, and *Nostoc commune* (often very large and abundant).

In the wettest hollows the pools are often constant and contain long shoots of *Hypnum pseudofluitans* (= *H. aduncum* var. *paternum*) as well as *H. aduncum* var. *intermedium*, *Potamogeton perfoliatus* and *Zannichellia pedicellata*, whilst in the surrounding marshy ground *H. aduncum* and its varieties *polycarpon*, *wheldoni* and *gracilescens*, *H. cuspidatum*, and *Pellia fabbroniana* are associated with *Hydrocotyle vulgaris*, *Epipactis palustris*, *Iris pseudacorus*, *Phalaris arundinacea*, *Juncus effusus*, *Glyceria aquatica*, *Holcus lanatus* (often with *Epichloe typhina* parasitic on it), and *Eleocharis palustris*.

An excellent account of these dunes is given by Moss (4). Some changes have occurred since that was written (1906) but they scarcely affect the conclusions arrived at. The association of strand plants was little evident for several years (probably owing to storms and high tides) but in 1916 appeared to be regaining its former conspicuousness.

THE LANCASHIRE SAND-DUNES

These have been briefly described by Tansley in *Types of British Vegetation* (6), and by Wheldon in *Some social Groups of the Bryophyta* (11). The northern dunes near Blackpool have lost many of their natural characters through building and drainage and call for no special mention, but those near Southport are remarkable in many ways. Like those of Braunton, they consist of ridges and furrows running parallel to the sea, but these ranges of sand-hills and valleys or "slacks" are more definite and numerous, though the enclosed slacks are not so large as those of Braunton.

The dominant moss on the hills is again *Tortula ruraliformis*, but *Camptothecium lutescens* is rare or absent, whilst the following species, which are less frequent or absent on the Devon and Somerset dunes, are abundant: *Brachythecium albicans*, *Barbula rubella* and *Ceratodon conicus*. Lichens are rare and in many cases appear to have been introduced during the planting of trees, *Peltigera canina* and *P. horizontalis* only occurring in the parts where planting has taken place. No Collemas, *Cladonia furcata*, *Urceolaria scruposa*, *Biatorina coeruleonigricans*, nor *Bilimbia sabuletorum* have been noticed, but *Arthopyrenia areniseda* and *Cladonia pyxidata* var. *poecillum* occur in some of the dune hollows.

A Harpidia association is well shown in the hollows which form pools during the winter months, the following species occurring: *Hypnum lycopodioides* a, *H. wilsoni* a, *H. revolvens* a, *H. aduncum* a, *H. pseudofluitans* (*H. aduncum* var. *paternum*) a, *H. intermedium*, *H. scorpioides*, *H. sendtneri*. Other species of *Hypnum* not belonging to the Harpidia group as *H. cuspidatum* and *H. giganteum* are sometimes abundant, whilst *Amblystegium filicinum* var. *whiteheadii* sometimes becomes the dominant partner. In hollows more of a marshy character *Hypnum elodes*, *H. polygamum* and var. *stagnatum*, *H. cuspidatum* and *Amblystegium filicinum* are the chief mosses. Many of these Hypna (*H. lycopodioides*, *H. wilsoni*, *H. scorpioides*, *H. revolvens*, *H. intermedium*) are usually plants of mountain bogs. Their occurrence in sand-dune pools may be explained by considering them as plants of an ascending series which have been almost eliminated in the lowlands by drainage and cultivation. *Hypnum lycopodioides* and *H. scorpioides* are now usually sub-alpine plants; the others, though they are much more frequent in mountain regions, have been more successful in their competition with plants of a lower range.

The Southport dunes are also remarkable for containing several other mosses which are usually found at higher altitudes; *Meesia trichodes*, *Swartzia inclinata*, *Catocarpium nigrum* and *Amblyodon dealbatus* are all found in the moist hollows of the sand-hills. They are considered as immigrants from their mountain stations (see (6), p. 352), but the preceding explanation of the presence of some Hypna may also apply to them. They have also been found on the Anglesey sand-hills (2).

SUMMARY

There are a number of associations represented on our western dunes with various others intermediate between dune associations and halophilous or salt-marsh associations.

The most abundant plants of the sand-hills are often mosses or lichens, the more or less unstable dunes being dominated by one or more of the following: *Tortula ruraliformis*, *Camptothecium lutescens*, *Brachythecium albicans*, *Cladonia furcata*, *Peltigera canina*, *P. rufescens*.

The wet hollows of the dunes often form an association of *Harpidia* (*Drepanocladus*), the damp hollows a Brya association.

The changes in mobility of the sand are well shown by the lichens, *Peltigera*s on the unstable hills and fruticulose lichens such as *Usnea*, *Ramalina* and *Evernia* on those which are almost fixed, an intermediate stage being shown by the abundance of *Cladonia furcata*.

Many calciphilous plants (e.g., *Barbula tophacea*, *Trichostomum crispulum*, *Pellia fabbronia*, *Preissia quadrata*, *Lophozia badensis*, *Scapania aspera*, *Camptothecium lutescens*) are present owing to the presence of comminuted shells.

On the inner dunes there are a number of plants which are found on all dunes, but the floristic composition varies with the character of the surrounding land.

Many of the bryophytes growing on the sand-hills have xerophytic characters, though none can be called xerophytes.

The Algae on the seaward portion of the dunes chiefly belong to the gelatinous Cyanophyceae; it is also to be noticed that the lichens on the outer dunes have a blue-green algal constituent, and are often gelatinous. The frequency of cyanophyceous algae and of lichens in which these are the algal symbionts cannot be explained by their tolerance of brackish water, since the algae do not form a conspicuous part of the marine flora, but is due to the power which the mucilage has for absorbing water.

Some of the dune bryophytes are only found elsewhere on mountains, drainage and cultivation having eliminated them in intermediate regions.

LISTS OF PLANTS OF SAND-DUNES

Association of Strand Plants

[See (6), p. 340, and (8).]

Sea-Couch-Grass Association

Agropyron junceum d.
Carex arenaria sd.
Glaucium flavum o.
Cochlearia officinalis o.

Cakile maritima f.
Arenaria peploides a.
Eryngium maritimum f.
Caucalis arvensis o.

Senecio vulgaris var. *radiatus* la.
Glaux maritima o.
Solanum dulcamara o.
Lycium chinense o.
Thymus serpyllum o.
Beta maritima o.
Atriplex hastata f.
A. deltoidea f.
A. babingtonii f.
Salsola kali f.
Rumex crispus o.

Euphorbia paralias o.
Holcus lanatus o.
Bromus hordeaceus var. *nanus* o.
Hordeum murinum var. *arenarium* o.
Trichostomum flavovirens a.
Tortula ruraliformis a.
Bryum intermedium o.
B. argenteum o.
B. erythrocarpum o.
Camptothecium lutescens a.
Brachythecium albicans a.

[Also see Travis in (8), in which paper the strand and fore-dune floras are joined together. The two associations run into each other on many other dunes.]

Sand-hills. Ammophiletum arenariae

(a) Very mobile hills

Ammophila arenaria d.
Euphorbia paralias o.
Sedum acre o.
Anagallis arvensis o.
Senecia jacobaea o.
Viola canina r.
Erodium cicutarium r.

Potentilla anserina r.
Leontodon hispidum r.
Nepeta glechoma r.
Teucrium scorodonia r.
Cynoglossum officinale r.
Bryum argenteum r.
Agaricus spp. r.

(b) Less mobile dunes

Ammophila arenaria d.

Euphorbia paralias a.

The phanerogamic plants found on the very mobile dunes become more frequent.

Viola curtisii f.
Arenaria leptoclados f.
Galium verum o.
Erigeron acre o.
Carlina vulgaris o.
Sonchus oleraceus o.
Oniscus lanceolatus o.
Ajuga reptans o.
Scrophularia nodosa o.
Iris foetidissima o.
Tortula ruraliformis d.
Camptothecium lutescens (sand-dune form) a.
Brachythecium albicans a.

Bryum pendulum f.
B. argenteum f.
B. inclinatum f.
B. caespiticiu o.
Ceratodon purpureus f.
Barbula convoluta f.
Trichostomum crispulum f.
T. flavovirens f.
Tortula ruralis o.
Peltigera canina a.
P. rufescens a.
P. spuria o.
Collema crispum o.

(c) Somewhat stable hills

[For Phanerogamic plants see preceding lists and (6), pp. 349, 350, etc.]

Tortula ruraliformis d.
T. ruralis r.

Camptothecium lutescens (sand-dune form)
a to d.

Bryum pendulum a.
B. argenteum f.
B. inclinatum f.
B. caespiticium o.
B. capillare o.
Ceratodon purpureus a.
C. conicus o.
Swartzia inclinata r and l.
Barbula convoluta (often almost black) a.
B. rubella a.
B. fallax, a and var. *brevifolia* a.
B. unguiculata o.
B. hornschuchiana o.
B. gracilis o.
B. vinealis o.
Eurhynchium megapolitanum r.

Brachythecium albicans a to sd.
B. glareosum o.
Peltigera canina a.
P. rufescens a.
P. horizontalis r.
P. spuria o.
Collema crispum f.
C. ceranoides o.
Leptogium pulvinatum o.
L. lacerum a.
L. scotinum var. *sinuatum* a.
L. tenuissimum r.
Cladonia furcata, a sometimes d.
Biatorina coeruleonigricans o.
Bilimbia sabuletorum o.

[For Fungi see Wheldon, (9).]

(d) Almost fixed sand-hills or banks of sand

The same species as in (c) but the characteristic members of the *Ammophiletum arenariae* are not so abundant and many other species appear. The additional phanerogams partly depend on local conditions. The following list gives the additional bryophytes and lichens, many of which must be considered as casual visitors.

Pleuridium alternifolium o.
Ditrichum flexicaule o.
Dicranella heteromalla o.
Acaulon muticum o.
Dicranum scoparium o.
Encalypta rhabdocarpa r.
E. streptocarpa r.
Trichostomum mutabile o.
 var. *cophocarpum* and var. *littorale* o.
T. fragile o.
Tortula subulata o.
Leptobryum pyriforme r.
Bryum roseum o.
B. atropurpureum r.
B. donianum r.
Thuidium philiberti r.
T. abietinum r.
Eurhynchium confertum o.
Amblystegium serpens o.
Olimacium dendroides f. *depauperata* o.
Hypnum cupressiforme and vars. *ericetorum*
 and *tectorum* a.
Brachythecium rutabulum f.

Hylocomium squarrosum f.
H. splendens o.
H. splendens var. *gracilius* o.
Lophocolea cuspidata f.
L. bidentata o.
Ptilidium ciliare r.
Frullania dilatata (often almost black) r.
Scapania aspera var. *inermis* o.
S. aequiloba o.
Cladonia pungens and f. *foliosa* f.
C. pyxidata and var. *pocillum* f.
C. fimbriata o.
Urceolaria scruposa f.
U. bryophila and f. *lichenicola* f.
Collema pulposum o.
C. cheileum r.
Squamaria crassa r.
Rhizocarpon petraeum (on small stones) r.
Usnea hirta o.
Evernia prunastri o.
Ramalina farinacea o.
Bacidia mustorum o.

"The grassland association of dune hollows" is, like the above, a transition to a dune pasture. The phanerogamic and cryptogamic flora is similarly variable. It differs chiefly from the above in the greater abundance of grasses and in the less xerophilous character of its flora. For phanerogams see *Types* (6), pp. 345, 352. Many plants are invaders from the surrounding district; *Tortula ruraliformis*, *Camptothecium lutescens* and *Brachythecium albicans* become less abundant, whilst *Hypnum cupressiforme*, *Brachythecium rutabulum*, *Eurhynchium confertum*, *Hylocomium squarrosum*, *Barbula convoluta*, *Ceratodon purpureus*, *Bryum capillare* and *Lophocolea cuspidata* are common members of the mossy carpet often found. Any of the plants mentioned in the preceding list may occur in this sub-association.

Dry Association of Salix repens

[See (6), p. 351.]

The bryophytes and lichens are similar to those of "(c) Somewhat stable hills," p. 139.

Riccia crystallina Association (Brackish Slacks)

Glaux maritima.
Riccia crystallina.
Collema glaucescens.

Collema pulposum.
Vaucheria sessilis.
V. dichotoma.

On similar slacks the following plants have been noted:

Arenaria peploides f.
Sagina maritima.
S. apetala var. *prostrata*.
Glaux maritima a.
Samolus valerandi.
Plantago coronopus var. *pygmaea* a.
Chenopodium rubrum.
Littorella lacustris f.
Rumex crispus var. *trigranulatus*.
Ammophila arenaria.
Bryum pendulum.
B. warneum.
B. argenteum.

Trichostomum flavovirens f.
Barbula tophacea.
Peltia heimi.
Peltia intermedia var. *littoralis*.
Amblystegium serpens var. *salinum*.
Riccia crystallina.
Aneura pinguis.
Collema glaucescens.
C. pulposum.
Arthopyrenia areniseda.
Vaucheria sessilis.
V. dichotoma.
Barlaea crouanii.

Ranunculus baudotii, *Zanichellia pedicellata*, and *Chara* spp. are present in pools.

Brya Association in Damp Sandy Hollows

The phanerogamic constituents are somewhat variable, and only some of the characteristic species are given in the list.

Salix repens la.
Sagina nodosa.
Cardamine pratensis.
Parnassia palustris and var. *condensata* lf.
Galium palustre.

Centaurium vulgare f.
C. pulchellum.
Orchis incarnata f.
Epipactis palustris f.
Juncus bufonius and var. *fasciculatus* f.

- Carex distans*.
C. hirta.
C. extensa.
C. arenaria.
C. flacca.
C. goodenovii.
Equisetum variegatum var. *arenaria*.
Selaginella selaginoides l.
Bryum warneum a.
B. intermedium f.
B. pallens f.
B. pseudotriquetrum and var. *compactum* a.
B. calophyllum r.
B. bimum o.
B. lacustre r.
B. neodamense r.
B. uliginosum o.
B. pendulum f.
B. marratii r.
Brachythecium salebrosum var. *palustre* (B. *mildeanum*) f.
Brachythecium rutabulum and f. *robustum* o.
Barbula tophacea a.
Ceratodon purpureus o.
C. conicus r.
Amblyodon dealbatus r.
Catoscopium nigrum lf.
Meesia trichodes l.
Pottia intermedia and var. *littoralis* r.
Funaria hygrometrica f.
Trichostomum flavovirens o.
Mnium cuspidatum o.
Hypnum chrysophyllum and var. *erectum* o.
H. cuspidatum o.
H. cupressiforme var. *elatum* o.
H. stellatum o.
H. riparium o.
Alicularia scalaris o.
Calypogeia trichomanis o.
Cephaloziella bifida o.
Lophozia badensis and var. *obtusiloba* f.
L. turbinata o.
Petalophyllum ralfsii f.
Aneura multifida.
A. sinuata.
A. pinguis f. *crassior* and f. *minor* f.
 var. *angustior* o.
A. incurvata r.
A. major (sand-dune form) f.
Preissia quadrata lf.
Pellia fabbronia lf.
Reboulia hemisphaerica.
Lophozia excisa f. *arenaria*.
Moerckia flotowiana.
Arthopyrenia areniseda.
Collema pulposum f.
Nostoc commune f.
Hygrophorus conicus i.
H. pratensis f.
Sphaerospora asperior o.
S. trechispora.

Dune Marsh Association

The dominant plant is often a *Hypnum* (*Harpidium*).

- Sagina nodosa* f.
Parnassia palustris lf.
Hydrocotyle vulgaris sd.
Galium palustre a.
Anagallis tenella sd.
Samolus valerandi f.
Glauz maritima o.
Mentha aquatica a.
Lycopus europaeus a.
Teucrium scordium l.
Littorella lacustris ld.
Juncus maritimus l.
J. effusus f.
J. acutus l.
J. glaucus o.
J. bufonius o.
Iris pseudacorus o.
Epipactis palustris o.
Orchis incarnata o.
Eleocharis palustris ld.
Carex spp. a.
Scirpus holoschaenus l.
Glyceria aquatica o.
Hypnum aduncum a.
 var. *pseudosendtneri* ld.
 var. *wheldoni* o.
 var. *aquaticum* o.
 var. *intermedium* a.
 var. *paternum* a.
H. sendtneri.
H. polygamum a.
 var. *stagnatum* f.

<i>H. intermedium</i> lf.	<i>B. neodamense</i> r.
<i>H. wilsoni</i> o.	<i>Pellia fabbronia</i> f.
var. <i>hamatus</i> lf.	<i>Moerckia flotowiana</i> f.
<i>H. lycopodioides</i> f.	<i>Cephalozia bicuspidata</i> o.
<i>H. scorpioides</i> o, var. <i>angustifolius</i> .	<i>Riccia crystallina</i> o.
<i>H. cuspidatum</i> f.	<i>Vaucheria sessilis</i> a.
<i>H. giganteum</i> o.	<i>Mougeotia</i> spp. a.
<i>Amblystegium filicinum</i> f.	<i>Tribonema bombycina</i> a.
var. <i>whiteheadii</i> la.	
<i>Bryum pseudotriquetrum</i> f.	Cyanophyceous algae a.

Many of the hollows contain water for a large portion of the year. In these *Hypnum lycopodioides* is often dominant and may be associated with any of the following:

<i>Zannichellia palustris</i> .	<i>H. cuspidatum</i> .
<i>Potamogeton perfoliatus</i> .	<i>H. revolvens</i> .
<i>Hypnum aduncum</i> , especially vars. <i>paternum</i> , <i>wheldonii</i> and <i>aquaticum</i> .	<i>H. intermedium</i> .
<i>H. wilsoni</i> and var. <i>hamatum</i> .	<i>H. scorpioides</i> .
<i>H. elodes</i> .	<i>H. giganteum</i> .
	<i>Amblystegium filicinum</i> var. <i>whiteheadii</i> .

Some of the pools are permanent and contain little besides Algae, species of *Chara* being dominant.

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ON THE ECOLOGY OF THE VEGETATION OF BRECKLAND

By E. PICKWORTH FARROW

VI. CHARACTERISTIC BARE AREAS AND SAND HUMMOCKS

(*With Plates III—VI*)

Characteristic areas bare of vegetation and curious loose pellets of turf occur on some of the grass heath areas of Breckland and also in the degenerating *Calluna* zones. The origin of these was very mysterious and puzzling for a long time. The bare areas are of very variable size, some being very small while others are much larger. The exposed sand of these bare areas is often dark in colour and the bare areas are usually at a slightly lower level than the surrounding areas.

It was at one time thought that the bareness of some of these areas might possibly be due to acid surface drainage soaking into them and killing the associated vegetation. But though this hypothesis appeared to explain the observed facts fairly well in the case of some of the bare patches, yet there were others which it did not explain at all well. Some of these were areas generally bare but possessing characteristic isolated convex patches of vegetation (see Photo 1, Plate III).

THE EFFECTS OF SAND BLASTS

Eventually however an area was discovered, bare generally, but possessing isolated areas of vegetation which were raised considerably above the general level of the bare area and the upper edges of which were undercut—roots being exposed—strongly suggesting the existence of a surface sand blast (see Photo 2, Plate III).

This particular area was therefore carefully examined during wind and the hypothetical surface sand blast was found to have a very real existence. The sand blast was especially apparent under a lens and when magnified the moving sand grains could occasionally be seen to tear a sand grain away from the isolated raised sandy masses.

In the advanced stages of these bare areas many flints are typically exposed on the surface owing to the sand which was once intermingled with them having been cut away and removed by the wind and by the sand blast of grains already moving.



Photo 1. SMALL BARE SANDY AREA ON CAVENHAM HEATH, ASSOCIATED WITH CONVEX TUFTS OF VEGETATION. The origin of these bare areas was long mysterious (see page 144). It was eventually discovered that they are caused by sand blasts, aided probably by rabbits scratching and loosening the surface sand in the first instance. Note the large quantity of rabbit dung.



Photo 2. MUSHROOM-SHAPED CUPOLA (SAND-BLASTED HUMMOCK) ON CAVENHAM HEATH. The sand blast has strongly undercut the edge of this hummock, exposing roots and producing a mushroom-shaped structure. These hummocks rise relatively to the surface of the soil largely by the wholesale cutting away and lowering of the latter. Note the large number of flints and fragments of *Calluna* roots and stems exposed on the surface of the soil. Eventually the cupola is completely severed and the loose pellets thus formed are often blown considerable distances.

FORMATION OF HUMMOCKS OR CUPOLAS AND OF LOOSE PELLETS

In the first stages when the sand blast on the surface is slight the vegetation of small isolated areas is often able to cope with it more or less and these form slightly convex raised areas which gradually become more and more convex owing to the deposition of sand from the general surface upon them (see Photo 1, Plate III). In this stage some of these convex raised areas resemble the cupolas of forts and possibly they tend to take on this characteristic and particular form owing to the bombardment to which they are subjected by the rapidly moving sand grains.

As the areas of sand blast around these cupolas become still more active the cupolas become more and more raised in section, the shoots of the plants rising up through the deposited material until the kinetic energy of the moving particles in association with the critical angle of the material prevents the sectional curves from becoming any more convex, the new moving material slipping down the sides of the cupolas and tending to remove some of the already deposited material.

After this the continued sand blast continues to cut away and lower the general surface of the substratum and leaves the now very convex cupolas, which were formerly closed on the general surface, standing on short columns of sand above the general surface of the substratum, chiefly owing to the roots beneath the cupolas tending to hold the sand grains together for a time and to prevent them from being cut away by the surface sand blast¹.

It will be seen that these particular vegetated sand cupolas of Breckland rise relatively to the surface of the substratum in a somewhat different manner from many sand hummocks, for the cupolas arise at first from the surface owing to sand being transported from the general surface immediately around and deposited on them among the plant shoots, so that while the general surface sinks the hummocks rise. Later on this process becomes much more pronounced as the general surface layers of the underlying substratum are cut away wholesale by the sand blast, leaving the hummocks standing relatively much higher than the new surface of the substratum on short columns of sand. Thus the Breckland sand cupolas rise relatively to the surface of the substratum largely by the wholesale cutting away of the substratum in addition to the deposition of sand on the tops of the cupolas themselves.

The Breckland sand cupolas may be compared with ordinary sand hummock plants at Blakeney on stable shingle banks on the landward side of the main dune ridges. Sand is carried by wind from these dunes and from the foreshore and is deposited amongst these plants, and thus the hummocks arise. But the Blakeney sand hummocks do not rise relatively to the general

¹ The extent to which typical sand cupolas of Breckland have become better developed during an interval of one year can be seen by a comparison of Photos 3 and 4, Plate XVIII, This JOURNAL, 3, Dec. 1915.

level of the substratum through wholesale cutting away of the latter as happens in the case of the Breckland sand hummocks.

Though the roots below sand cupolas hold the immediately underlying sand together for some time after the general surface of the surrounding sand has been cut away and lowered by the sand blast, yet when the general surrounding surface is sufficiently lowered, the surface sand blast eventually undercuts the edges of the cupolas beneath many of the roots (see Photo 2, Plate III) and this undercutting often proceeds until the upper portions of the cupolas and the roots underneath them are completely cut off by the surface sand blast from the substratum, and these cut-off cupolas with roots are often blown by the wind to considerable distances. This is the origin of those curious and characteristic loose pellets of turf which occur in various places and which had previously been so mysterious and puzzling.

RETROGRESSION OF THE VEGETATION ON CUPOLAS

The structural changes in the formation and undercutting of the cupolas are reflected in changes in their vegetation.

One of the most important changes in the vegetation of the cupolas as they become more convex and rise relatively to the substratum is the following: *Agrostis vulgaris*, which was previously co-dominant with *Festuca ovina* before the cupolas began to rise, gradually loses its co-dominance and *Festuca ovina* becomes the sole dominant. This change in the vegetation of a rising cupola is of considerable interest in view of the fact that when the ordinary grass heath was experimentally irrigated the reverse change took place, *Festuca ovina* losing its co-dominance and *Agrostis vulgaris* becoming the sole dominant¹. The result of the irrigation experiment may rather tend to suggest that this change in the vegetation as a cupola rises, *Agrostis vulgaris* losing its co-dominance and *Festuca ovina* becoming the sole dominant, is very likely largely due to the hummock becoming gradually drier as it rises and becomes undercut by the sand blast, since the change in the vegetation is the reverse of that which occurs in the vegetation when the ordinary grass-heath is experimentally irrigated.

As the small hummocks gradually become taller and undercut from the substratum owing to the sand blast across the surface of this underlying stratum, various mosses (principally *Campylopus flexuosus* and *Ceratodon purpureus*) become dominant on the central portion of the upper surface of the hummocks, and later on, when the hummocks are just about severed from the substratum, various lichens (principally *Cladonia coccifera*, *Cl. cervicornis*, *Cl. uncialis* and *Cetraria aculeata*) usually become established on the tops of the hummocks, a ring of just living *Festuca ovina* frequently remaining round the edge of the cupolas, so that the same cupola frequently exhibits zoned vegetation corresponding to the last three stages of this retrogressive

¹ Part IV, "Experiments relating to the Available Water Supply." This JOURNAL, 8, p. 109.

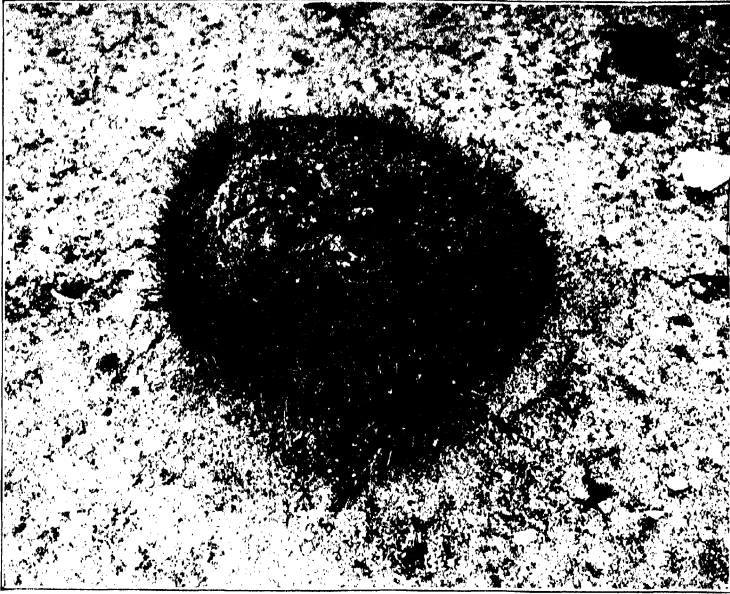


Photo 3. ZONATION OF VEGETATION ON A BRECKLAND SAND CUPOLA. As a cupola is undercut a true retrogressive succession takes place in its vegetation probably owing to diminution in available water supply. In the case shown a ring of *Festuca ovina* remains round the edge, just above is a moss zone occupied chiefly by *Campylopus flexuosus* and *Ceratodon purpureus*, while the top of the hummock is a lichen zone occupied by *Cladonia uncialis* and *Cetraria aculeata*. (See page 146.)

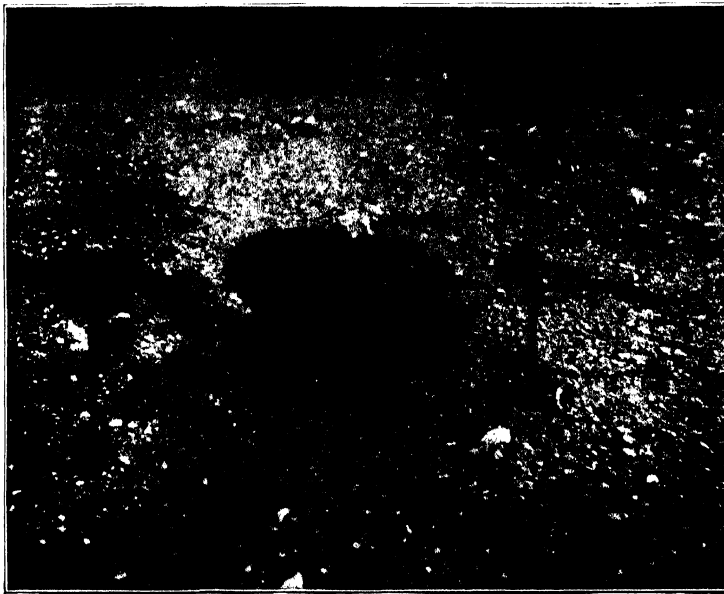


Photo 4. ROOT OF A DEGENERATE *Calluna* PLANT EXPOSED THROUGH PARTIAL DISINTEGRATION BY THE SAND BLAST OF A ONCE LARGER CUPOLA. The sand blast is here tearing away the cupola itself before finally undercutting the remains. On the right of the hummock a degenerate *Calluna* plant with bare roots can be seen. This once formed part of the hummock. (See p. 147.)

succession on its surface (see Photo 3, Plate IV), the various zones gradually expanding outwards as the cupola becomes gradually drier.

It will be seen that the stages of this succession are as follows:

1. *Agrostis vulgaris* and *Festuca ovina* co-dominant.
2. *Festuca ovina*, sole dominant.
3. Moss stage (*Campylopus flexuosus*, *Ceratodon purpureus*, etc.).
4. Lichen stage (*Cladonia coccifera*, *Cl. cervicornis*, *Cl. uncialis* and *Cetraria aculeata*).

This is a true retrogressive succession—probably chiefly in relation to water supply—and it is a very good case, as it is comparatively rare to have a true retrogressive succession passing through four stages.

Sometimes these nearly severed hummocks topple over on one side before being blown away by the wind, and when this happens any ring of living *Festuca ovina* around the edge of the cupola comes into contact with the sandy substratum and, since the hummock usually falls on the lee side, *Festuca* often roots and grows in the underlying sand. Wind blown sand is frequently deposited amongst this newly rooted *Festuca* on the sheltered side of a toppled over hummock, producing a miniature *Festuca ovina* dune on the leeward side (cf. the deposition of sand on the leeward side of developing sand-dunes). Soon however the fallen over hummock is usually either blown away or gradually disintegrated *in situ* by the sand blast and the newly rooted *Festuca* on the surface of the substratum is then exposed to the full force of the sand blast which quickly kills it.

RELICS OF *CALLUNA* IN CUPOLAS

In the case of fairly large cupolas, the sand blast usually cuts away and disintegrates much of the cupola itself before finally undercutting the remains (this is well illustrated in Photos 4 and 5). In the case of the formerly larger cupola seen in Photo 4 the disintegrating and tearing effect of the sand blast on the cupola itself before it finally undercuts the remains can be well seen on the right hand side of the cupola where the vegetation is being gradually destroyed and much loose sand is exposed. The sand blast has already cut away a considerable portion of this cupola and has exposed the root of a degenerated *Calluna* plant which still remains fixed in the substratum in its vertical position at some little distance from the remains of the disintegrating cupola. This plant was once contained inside the formerly larger grass heath (degenerated *Calluna* heath) cupola before the sand around it had been torn away by the sand blast.

Sometimes many portions of the roots of the *Calluna* plants which once occupied these particular grass heath areas, before the original *Calluna* heath degenerated to grass heath through rabbit attack, can be seen remaining fixed *in situ* in the lower portions of isolated grass heath cupolas. In such cases owing to the presence of the numerous tough *Calluna* roots below the cupolas

the sand blast cannot undercut the cupolas so readily as it usually can and often begins to disintegrate the upper portions of the cupolas before finally disintegrating or undercutting the remains.

LARGER HUMMOCKS AND SECONDARY HUMMOCKS

Probably owing to local variations in intensity of sand blast and to other local conditions, considerably larger and taller hummocks are sometimes formed. The vegetation on the upper surfaces of these larger hummocks also passes through the retrogressive succession which has already been described, and eventually when the upper surfaces of these taller hummocks are very dry and rather bare of vegetation the surface layers usually become gradually torn away by the wind and sand blast. This process of the gradual disintegration of the dry upper surfaces of the taller variety of hummocks also frequently exposes fragments of *Calluna* roots, which are all that remain of the former *Calluna* heath that previously occupied these isolated remnants of the higher grass heath surface.

It has already been mentioned that as the smaller varieties of hummocks gradually become undercut the *Festuca ovina* on the tops of the hummocks gradually dies and becomes replaced by various mosses (*Campylopus flexuosus*, *Ceratodon purpureus*, etc.) and eventually largely by lichens (*Cladonia coccifera*, *Cl. cervicornis*, *Cl. uncialis* and *Cetraria aculeata*, etc.). Sometimes in these cases, when the upper surfaces of the primary hummocks are very dry owing to the hummocks being badly undercut by the sand blast across the surface of the substratum, these dry upper surfaces also become sand blasted so that bare sand becomes exposed, and small secondary moss and lichen hummocks filled with sand may form on the upper surfaces of the primary hummocks (see Photo 5, Plate V). Sometimes these smaller secondary moss and lichen hummocks on the dry upper surfaces of badly undercut primary hummocks also have their edges undercut by the sand blast across the upper surfaces. (See Photo 5.)

RECOLONISATION

Sometimes, probably owing to unexplained variations in the local conditions, the sand blast across a sand blasted area ceases, and when this happens the cupolas on that area remain fixed and dormant and the intervening bare areas become recolonised. The chief agents in this colonisation of bare sand blasted areas are: *Polytrichum piliferum*, *Campylopus flexuosus*, *Cladonia coccifera*, *Cl. cervicornis*, *Cl. uncialis* and *Cetraria aculeata*.

BREAKING OF RECOLONISED SURFACE

Often the surface layers of these formerly sand blasted areas which have become colonised by mosses and lichens break up into small pieces and these small pieces are blown away by the wind, thus exposing a fresh surface which

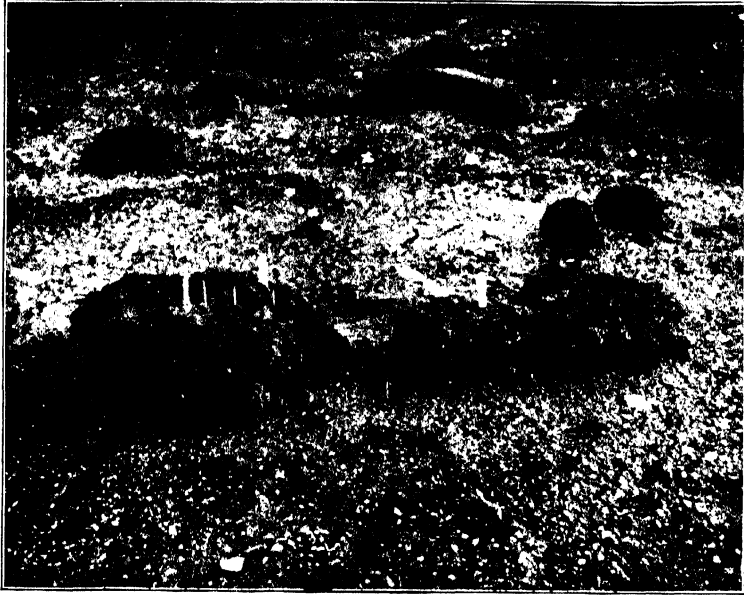


Photo 5. UNDERCUT GRASS HEATH HUMMOCKS BEARING SECONDARY MOSS AND LICHEN HUMMOCKS ON THEIR SAND-BLASTED UPPER SURFACES. As a result of the desiccation of a primary hummock by the undercutting of its edges, the upper surface itself often becomes sand blasted and small secondary moss and lichen hummocks may then arise on this. On the left-hand primary hummock the secondary hummocks are also seen to be undercut. (See p. 148.)



Photo 6. ANCIENT SAND-BLASTED AREA COLONISED BY *CAMPYLOPUS FLEXUOSUS* AND SUBSEQUENTLY BROKEN INTO SMALL PIECES. When the sand blast across an area ceases the area becomes colonised by various mosses and lichens and is often afterwards broken up into small pieces (see p. 148). Seven old, now dormant, cupolas are seen in the photograph.

may again become colonised. A good example of a formerly sand blasted bare area on which the sand blast has become dormant and the surface of which has become colonised by *Campylopus flexuosus* and which has subsequently become broken up into small pieces is seen in Photo 6 (Plate V). Seven ancient formerly sand blasted (now fixed) cupolas are seen in this photograph.

Before their origin and history were discovered, these particular local broken up mossy areas—so different from the surrounding vegetation—were very mysterious phenomena.

CAUSES OF SURFACE CRACKING AND FORMATION OF SURFACE SCALES

This process of breaking up of the upper strata and scale formation on colonised surfaces is very widespread and of considerable interest. It occurs at Blakeney. The causes of it are not definitely known, but it usually occurs in the surface layers where there are many fibres of the colonising plants and the presence of these fibres would tend to enable the surface layers to withstand tensile stresses in addition to being able to withstand compression stresses, while the lower layers devoid of fibres would chiefly be able to withstand compression stresses alone (cf. reinforced and ordinary concrete). It appears probable that this breaking off of the surface layer from the lower layers has to do with its different capacity for withstanding tensile stresses. This view may be explained as follows:

When the surface soil which previously occupied a certain volume contracts to a smaller volume owing to drying it frequently cracks along lines of weakness where the total tensile stress is greater than the tensile strength of the material. When this happens the upper strata of the soil break up into blocks separated by irregular fissures on the surface but remaining connected below. This is a common phenomenon in dry weather in clay soils and in other soils which—owing to the possession of a certain number of root fibres or other causes—can withstand a certain amount of tensile stresses without breaking down into small fragments. This phenomenon is often a nuisance in agriculture, because mustard (*Brassica nigra*, *B. alba*), charlock (*B. arvensis*), and other oily seeds, fall down the fissures, and do not germinate in autumn in time to be killed by autumn cultivation, but remain dormant sometimes for many years, and then germinate and grow luxuriantly as weeds when the land is deeply ploughed.

With regard to the formation of loose surface scales on colonised surfaces after some of the lower strata have broken up into vertical blocks, or even in some cases while the lower strata remain longitudinally connected (as in the case of the lower sandy soil in Photo 6, which cannot withstand tensile stresses without breaking down into minute fragments), the upper surface stratum of the soil contains many fibres of the colonising plants running in various directions. These fibres would enable this surface stratum to withstand a certain amount of internal tensile stress and to contract and expand as a unit within certain limits. The upper layers of this surface stratum are dried by sun and wind and contract more rapidly and before the lower layers. Owing however to the existence of the fibres of the colonising plants running in all directions between these limits the lowest layers of the surface stratum are forced to contract by the tensile stresses at the average rate of contraction of the unit, i.e. at the normal rate of contraction of a layer considerably above them.

The upper layer of the substratum, however, which lies immediately below the lower layers of the surface fibre-containing stratum, does not contain many fibres itself and so it can contract at the normal rate of contraction of a layer at its level. Since however the lower layers of the surface stratum lying immediately above it are forced by the possession of fibres and greater average contraction of the surface stratum to contract at

the average rate of contraction of the upper surface stratum, i.e. much more rapidly than the upper layer of the substratum, a considerable transverse or shearing stress is produced between these two layers, and, since there are relatively few fibres connecting them, the lowest layer of the surface stratum may be sheared off from the substratum and thus produce loose surface scales. This is the probable explanation of the common phenomenon of the production of loose surface scales on various soils in dry weather.

Later on the upper layers of the loose surface stratum may become considerably drier and tend to contract far more than the lower layers of this loose stratum, with the result that the tensile stresses along the upper zone of the surface stratum become considerably greater than the tensile stresses along the lower zone. When this difference in the longitudinal stresses becomes sufficiently great the loose surface scale may eventually curl upwards especially at its edges. This phenomenon of the curling up of the loose surface scales is very common in various places—for instance on some of the mud flats at Blakeney—especially on those which are only occasionally covered by the tides.

BARE AREAS BETWEEN RABBIT-EATEN *CALLUNA* BUSHES

In addition to the characteristic bare areas which occur on the grass heaths and the origin of which was puzzling but has now been explained, bare areas sometimes occur between rabbit-eaten *Calluna* bushes (see Photo 7). The origin of these other bare areas had also been mysterious and various abortive hypotheses had been invented to account for them, but when it was discovered that the bare areas on the grass heaths were due to sand blasts, it was thought that the bare areas which sometimes occur between rabbit-eaten *Calluna* bushes might also be due to sand blasts. If this were so, small cupolas like those found on the bare areas on the grass heaths might also be expected to occur on the bare areas between rabbit-eaten *Calluna* bushes, and in certain places small cupolas were found (see Photo 7) although they had not been seen before a special search was made. The discovery of these characteristic cupolas on the bare areas between *Calluna* bushes indicated that the bareness in these instances was also due to a sand blast, and on examination during wind the existence of a sand blast was demonstrated. The cupolas are not common on the bare places between *Calluna* bushes—apparently because the sand blasting action has usually gone so far that all the cupolas have been cut off from the surface and blown away.

The past history of these particular areas (such as that seen in Photo 7) is probably as follows. These areas were once typical *Calluna* heath but the *Calluna* gradually degenerated through rabbit attack in the way that has been described and grass heath came to occupy the spaces between the *Calluna* bushes. As the bushes became more and more eaten down by the rabbits, the wind would eventually reach the surface of the intervening spaces and start the sand blast, probably in the first instance with the help of rabbits scratching the surface sand and loosening some of it. From a mathematical point of view it is difficult to see how wind alone could raise a sand grain into the air. A loose grain could however be driven up and along a surface by the wind, and on hitting against stationary grains would not only start them moving but



Photo 7. BARE AREAS BETWEEN RABBIT-GRAZED *CALLUNA* HUMMOCKS. The bareness of the ground between the hummocks is here also due to sand blast. Small grass heath cupolas like those figured in Plate III are seen in the foreground. The whole bare area between the *Calluna* hummocks was probably once covered with grass heath arising from *Calluna* heath through rabbit attack. (See p. 150.)

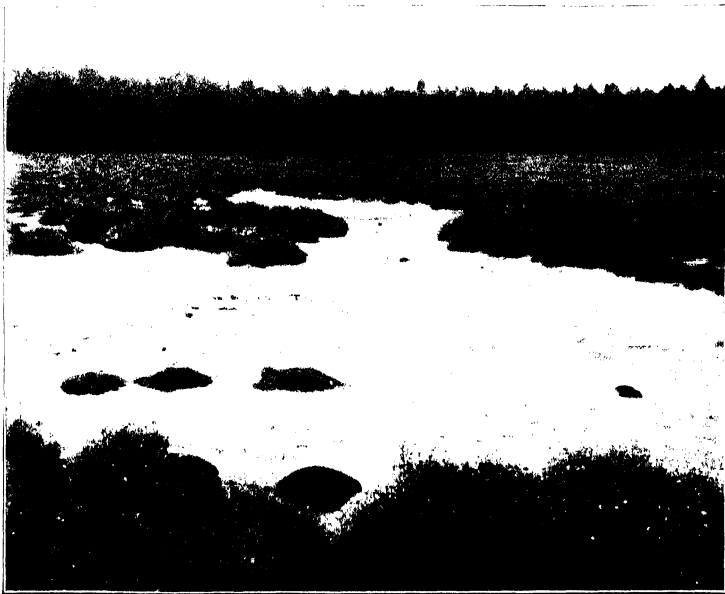


Photo 8. SAND-BLASTED AREA ON WEST NEWTON HEATH, NORTH-WEST NORFOLK. Three closely rabbit-grazed hummocks of *Erica tetralix*, filled with wind-blown sand, are seen in the middle of the bare area. By attacking the *Erica* on the edge of the bare area the rabbits probably lead to the extension of the area. (See p. 152.)

might itself shoot up at an angle. When the wind starts a sand grain moving this hits against other sand grains on the surface and starts these moving, and these in their turn start other grains moving and so on. Thus when once the sand blast has started its area tends to spread indefinitely.

The sand blasts which have become started amongst these eaten down *Calluna* hummocks have thus become wider and wider and have cut away most of the grass heath surface which had previously come to occupy the spaces between the eaten down bushes until nothing is left of it except isolated cupolas and hummocks (Photo 7, Plate VI). It would probably never have been suspected that grass heath had ever occupied the now bare intervening spaces between these rabbit-eaten *Calluna* bushes if it were not for these traces of the previous grass heath surface which are left behind in some cases although they have usually all been cut off by the sand blast and blown away by the wind.

Some of the sand which is carried away from the surfaces of the intervening spaces is deposited inside the neighbouring *Calluna* bushes, which are often full of sand. The rabbits usually eventually nibble the stems of the *Calluna* bushes down close to the level of the contained sand, producing very smooth rounded hummocks such as those seen in Photo 7, Plate VI. The smoothness of the surfaces of these hummocks is chiefly due to eating down of the *Calluna* stems by the rabbits nearly to the level of the contained sand and is not due to the sand blast as such, for the hummocks are practically as smooth on the side exposed to the prevailing wind and sand blast as on the sheltered side.

Sometimes in the case of very small *Calluna* hummocks which have been eaten down very closely by the rabbits all the contained sand is eventually swept out by the wind, exposing the bare *Calluna* stems.

Surface sand blasts and their resulting effects on the associated vegetation are of fairly widespread occurrence in Breckland. Probably as *Carex* and *Pteris* spread over the areas these plants will largely prevent sand blasts by binding the sand together and sheltering it from wind; but *Carex arenaria* apparently cannot prevent sand blasts in all cases, for sometimes its rhizomes are laid bare by them.

Sand blasted areas on West Newton Heath

Fairly large sand blasted areas also occur on some of the north-west Norfolk heaths. Such an area on West Newton Heath near Sandringham is shown in Photo 8, Plate VI. This heath is largely an *Erica tetralix* heath and is much damper than most of the Breckland heaths; but probably for the existence of a sand blast it is only necessary that the sand grains lying immediately on the surface should be temporarily desiccated. The three smooth and rounded *Erica tetralix* hummocks, filled with wind blown sand from the surrounding sand blasted area and closely eaten down by rabbits, on the bare area in Photo 8 strongly resemble the smooth and rounded rabbit-

grazed *Calluna* hummocks of Breckland, filled with wind blown sand, such as those seen in Photo 7. The curious small tufts of taller flowering *Erica* stems on the left hand side of the otherwise smooth rabbit-grazed central *Erica tetralix* hummock seen in Photo 8 are probably caused by the rabbits preferring to continue to eat the young terminal growing portions of the already severely eaten down *Erica* shoots rather than the older and tougher portions of taller shoots which have, so to speak, got out of control. The *Erica tetralix* plants around the edge of the sand blasted area in the foreground and on the right hand side of Photo 8 are closely eaten down by the rabbits and filled with wind blown sand, whilst the *Erica* further away from the bare area is not closely eaten down. Probably the rabbits can reach the *Erica* on the edge of the bared area more readily than the *Erica* which is further away from the edge. If this be the case it reminds one of the greater degeneration of *Calluna* heath from rabbit attack along trackways than elsewhere¹. Probably the rabbits by eating the *Erica* on the edge tend to help or enable the sand blasted bared area to increase in size, even if they did not originate it.

An extensive area of *Erica tetralix* on West Newton Heath can be seen in Photo 8. It has already been mentioned that although there are far fewer rabbits on this heath than on most of the Breckland heaths yet owing to the fact that much of the vegetation now-a-days consists of the unpalatable *Erica tetralix* the actual rabbit *pressure* on the vegetation is far greater than that on most of the Breckland heaths, and any more attractive associates of these unpalatable plants would quickly be exterminated by the rabbits. Thus the extensive distribution and the purity of the unattractive *Erica tetralix* association on West Newton Heath are probably largely due to the cumulative effect of the rabbit pressure in killing off any more attractive competitors of these unpalatable plants more and more rapidly as they became rare until they were eventually exterminated².

In addition to occurring in Breckland and on the north-west Norfolk heaths bare areas resulting from sand blasts occur on some of the Surrey heaths near Blackheath and on various other sandy English heaths.

¹ See Part II. This JOURNAL 4, p. 64.

² See Part III. This JOURNAL, 5, p. 18.

REVIEWS

Guppy, H. B. "Plants, Seeds, and Currents in the West Indies and Azores." Pp. viii and 531, with 3 maps and a frontispiece. London, Williams & Norgate, 1917. 25s. net.

Mr Guppy's latest work consists of a series of special studies undertaken by him since 1906 in further elucidation of the problems of the oceanic dispersal of plants which have occupied his attention for so many years¹. The larger part of the present work is occupied with a study of West Indian plant drift, in the first place an analysis of the drift itself, an account of West Indian drift recorded from European shores, and a discussion of the Atlantic currents as elucidated by the tracks of floating bottles. The main conclusion in regard to Atlantic drift is that a complete circuit is possible: from the West Indies to the west European coasts in the Gulf Stream, then southward in the Canary Current to the neighbourhood of the Cape Verde Islands, and thence westward across the Atlantic to the Antilles by the North Equatorial Current. But in spite of this circulation and the consequent theoretical possibility of interchange of littoral plants between the Old World and the New, the effective distribution of plants by floating seeds from the New World to the Old is almost if not quite negligible, because the Gulf Stream impinges on shores where tropical seeds cannot establish themselves, and but little belated drift can find its way southward to the tropical West African Coast. On the other hand a large amount of drift must pass from the west coast of Africa to the north coast of South America and the West Indies in the South (or Main) Equatorial Current, and it is in this way that the similarity of the West Indian and West African littoral floras is to be explained. Nearly 90 per cent. of the littoral, estuarine, and riverside plants common to the Old and the New Worlds could be transported by the Equatorial Currents, as is shown by the capacity of the seed or fruit to float and remain viable for two to three months in sea water. On the other hand only 24 per cent. of a somewhat restricted list of those confined to the New World have seeds or fruits which will pass this test. If the list were extended, the proportion possessing floating seeds or fruit would no doubt be markedly diminished. In certain individual cases the evidence of distribution is difficult to harmonise with the suitability of the seeds or fruits for ocean traverse and the power of the currents to disperse them, but the great bulk of the evidence is quite decisive in favour of Mr Guppy's conclusions.

In regard to the question of the "adaptation" of floating mechanisms of seeds or fruits to the dispersal of littoral plants Mr Guppy is in general agreement with Schimper's conclusions, viz. that the plants take advantage of having seeds which have become buoyant from other causes—"Buoyancy, whether of seed or fruit, is quite accidental as far as adaptation to dispersal is concerned. It is just as likely to be developed in inland plants, especially where dry conditions prevail; and it is shown that in such cases, where the plants are xerophytes, they tend to gather at the coast. But it is only the littoral station that determines its utility for dispersal, since it brings the plant with buoyant seeds or fruits within the influence of the currents" (p. 229). This subject is dealt with more in detail in the author's previous work, *Plant Dispersal*.

Mr Guppy devotes several chapters to a detailed record of the drift met with on the Turks Islands, a small group of the Bahamas, which he chose to investigate because they

¹ See "Dispersal of Plants as illustrated by the Flora of Keeling Atoll," *Journ. Victoria Inst.* London, 1889. *Plant Dispersal*, London, 1906. "Plant Distribution from an Old Standpoint," *Trans. Vict. Inst.* 1907. "Distribution of Plants and Animals," *Petermann's Mitteilungen*, 1910 *Studies in Seeds and Fruits*, 1912.

furnish a good sample of the West Indian drift on the first stage of its journey in the Gulf Stream. Other chapters are devoted to the geology and flora of the Turks Islands. The islands are formed of calcareous æolian sandstone and blown sand and present an intensely xerophytic habitat. The smaller "cays" are mainly stocked with West Indian strand plants, the larger islands possessing in addition a sparse scrub of Bahama species. "Not a few of the shore plants invade the inland plains, some of them having almost deserted the beach," and "the plants of the inland scrub may in their turn intrude on the beach, mingling there with the characteristic strand flora. Here the xerophytes of the plain and the xerophytes of the strand experience little difficulty in exchanging their stations, the influences that tend to keep them apart being more concerned with fitness for dispersal by currents than with station." "Two thirds of the littoral plants [of the Turks Islands] that are found in the Old World could have been directly brought there by the currents. For the shore plants confined to the New World, we have usually to appeal to the bird, to the drifting log, and to man. In the case of the inland scrub plants birds are probably the chief agents of distribution."

A chapter is next devoted to "the current connexions of the Southern Ocean" and here is described the steady eastward drift with a slight northerly trend in the latitude of the "roaring forties." From the evidence of drifting bottles and wreckage it is shown that Fuegian drift, for instance, would be largely intercepted by Australia, Tasmania and the northern part of New Zealand: drift from the southern extremity of New Zealand would be stranded on the shores of southern Chile; and only drift from the southernmost of the Antarctic Islands would be likely to clear the Horn. The complete circuit of the globe in these latitudes would take rather more than three years. On the other hand drift from tropical north-west Australia and from Malaya would cross the Indian Ocean to tropical East Africa, and from south-east Australia drift would go to New Zealand; but no Australian drift could cross the Pacific to America on account of the westerly set of the currents between the North Cape and Fiji. Pacific American equatorial drift would reach north-west Australia through the South Equatorial Current. South African drift might reach South Australia. Broadly, southern drift travels west in tropical latitudes and east in temperate latitudes. While in the Indian and Atlantic Oceans the littoral and estuarine floras of the opposite sides are closely similar, the distribution has been retarded in the Pacific by the great width of that ocean and the paucity of suitable stopping places in the form of islands that would support a mangrove flora. These conclusions are in agreement with Hedley's results based on the general faunistic and floristic relations of Australasia and South America.

A very interesting chapter on the influence of the divergence of the continents on the distribution of *Sphagnum* and *Carex* brings out the striking increase of endemism in both these genera as we pass from the great land masses of the northern hemisphere into South America, Africa, and southern Asia and Australia respectively, supporting the author's general view of southward migration, with consequent geographical and taxonomic divergence, of the great plant stocks.

The three chapters on the Azores which conclude the book contain an excellent account of the flora and vegetation of this group of islands and their relationships with other regions. The author calls attention to the strong probability that of the existing flora less than 200 species out of the 560 flowering plants recorded by Trelease are really indigenous, and to the confusion resulting from Watson's ignoring this state of things. Mr Guppy describes in detail the zonation of the vegetation on the great volcanic cone of Pico (7613 feet). The zones he recognizes correspond fairly closely with those described by the older investigators of the Azorean flora, Hochstetter, Seubert and Morelet. Two zones are made of the laurel woods, perhaps the most characteristic feature of all the Macaronesian Islands. Mr Guppy's arrangement is summarised in the annexed table.

TABLE SHOWING DISTRIBUTION OF VEGETATION ON THE MOUNTAIN OF PICO (7613 feet).

Altitude	Climate	Vegetation
5500-7000 feet	Strong insolation, wide range of temp., strong winds, snow in winter	CONE OF PICO (scantly vegetated lava and cinders). Mats of <i>Calluna vulgaris</i> and <i>Thymus serpyllum</i> var. <i>angustifolius</i> . Tufts of <i>Menziesia polifolia</i> , <i>Polygala vulgaris</i> , <i>Agrostis castellana</i>
4500-5500 feet scrub zone	Cloud belt (rainy zone)	<p>UPPER WOODS (Juniper zone). <i>Juniperus oxycedrus</i> var. <i>brevifolia</i>, <i>Daphne laureola</i>, <i>Euphorbia stygiana</i>, dominant. <i>Taxus baccata</i>, lower levels, nearly extinct. <i>Dicksonia culcita</i>, <i>Acrostichum squamosum</i>, <i>Arceuthobium oxycedri</i> (on Juniper). Also <i>Erica azorica</i>, <i>Laurus canariensis</i>, <i>Myrsine africana</i>, <i>Ilex perado</i>, <i>Vaccinium cylindraceum</i>, common to these and the lower woods.</p> <p>UPLAND MOORS (2000-4000 feet). <i>Pteris aquilina</i>, <i>Polytrichum</i>, <i>Sphagnum</i>, dominant. <i>Erythraea massoni</i>, <i>Lysimachia nemorum</i> var. <i>azorica</i>, <i>Luzula purpureo-splendens</i>, <i>Calluna vulgaris</i>, <i>Menziesia polifolia</i>, <i>Polygala vulgaris</i>, <i>Potentilla erecta</i>, <i>Thymus serpyllum</i> var. <i>angustifolius</i> (drier areas). <i>Anagallis tenella</i>, <i>Hydrocotyle vulgaris</i>, <i>Viola palustris</i> (wetter areas).</p>
2000-4500 feet wood zone		
Sea level to 2000 feet. Up to 1500 feet the ground is largely under cultivation		<p>LOWER WOODS (Faya zone). <i>Myrica faya</i>, <i>Erica azorica</i>, <i>Laurus canariensis</i> (<i>Persea azorica</i>) dominant. <i>Ilex perado</i>, <i>Rhamnus latifolius</i>, frequent, <i>Persea indica</i>, <i>Piconia excelaa</i> (now rare). <i>Myrsine africana</i>, <i>Vaccinium cylindraceum</i>, <i>Hypericum foliosum</i>, <i>Viburnum tinus</i>, <i>Hedera canariensis</i>, <i>Smilax</i> sp., <i>Rubus fruticosus</i>, <i>Osmunda regalis</i>. [<i>Calluna vulgaris</i> and <i>Thymus serpyllum</i> var. <i>angustifolius</i> reach the coast on the old lava flows.]</p>

ZONE OF LAUREL WOODS

The upland moors, which are now used as pasturage for cattle, have been very largely extended by the disforestation of the slopes of the mountain. Mr Guppy shows that the woods were originally much loftier than at present, when trees over 30 feet high are rare. Eruptions and utilisation of wood in earlier times for building were the causes of great destruction of the forests, while the continued demand for firewood has resulted in the trees rarely being allowed to attain any considerable age or height. That the Juniper ("cedro" of the islanders) once attained considerable dimensions is proved by various evidence.

Comparing this zonation with that seen in Madeira and the Canaries, we find the laurel wood zone, which extends to sea level in the Azores, shifted upwards in these islands in correspondence with the more southern latitude. The lowest 2000 or 2500 feet at Tenerife is the "African" zone with cactoid Euphorbias, shrubby Compositae such as *Kleinia neriifolia*, and fleshy Crassulaceae, as well as *Phoenix canariensis* and *Dracæna Draco*. Above the laurel belt we enter, at about 5000 feet, the Pine belt (*P. canariensis*) and this was also the zone of *Juniperus oxycedrus*, now almost exterminated. At about 6500 feet the pine belt gives place to the zone of the leguminous shrub *Adenocarpus viscosus*, extending to about 7000 feet, and above this again the "retama" zone of *Spartocytisus nubigenensis*. In Madeira the African zone occupies the lowest 700 feet or so, and contains the Dragon tree, *Euphorbia piscatoria*, species of *Sempervivum*, etc. Laurel woods originally clothed the slopes from this level up to between 5000 and 6000 feet. The Juniper probably flourished in this at levels above 3000 feet. Indigenous pines are absent.

With regard to the stocking of the Macaronesian Islands, in the case of the Canaries, and to a less extent of Madeira, there were early invasions of African, Asian and later of American elements. Most of the peculiar Canarian genera appear to be connected with these early African and Asiatic invasions, by which the Azores were little affected. Later came an influx of the Mediterranean genera which now give character to the laurel woods of all three of the Macaronesian groups. These plants or their congeners, as Hooker pointed out, are abundant in the Tertiary strata of many parts of Europe—in the case of *Laurus canariensis* the same species. Other plants of the laurel woods still exist in Europe and the Atlas, and the influx of these, as well as of the plants of the upland moors of Pico is presumably still in progress.

The main means of transport, Mr Guppy concludes, have been birds—the wind being incapable, in the author's view, based on Mr Lloyd Praeger's experiments on the rate of fall of seeds, of transporting even the smallest seeds, as distinct from the spores of cryptogams, for long distances over the ocean. The woods of the Azores have been mainly stocked by frugivorous birds such as pigeons, and the link with Europe has been broken or is breaking, thus leading to the differentiation of new species or varieties both of the pigeons and of the plants they carried. The uplands on the other hand are mainly occupied by plants with small seeds which would probably be transported in the mud adhering to birds' feet or sticking to their plumage. In the case of the moor plants, and even more markedly in the case of the freshwater aquatics and sub-aquatics, this kind of transport is probably still going on and the species are identical with European ones. The coast flora, which is scanty owing to the rocky nature of most of the coast, has not been mainly brought by current drift as in the tropics. With the exception of those of *Crithmum maritimum* and *Ipomœa carnosa* all the seeds or fruits sink at once or very shortly. Drifting logs, and gulls or other seabirds, are appealed to as being the most likely means of arrival of the coast flora. Here again of course the connexion with the outside world is still maintained, practically all the species being common north temperate coast plants.

The whole of Mr Guppy's work, of which we have only attempted to notice some chapters of most interest to the ecologist, is packed with first-hand observations and will be indispensable to all students of plant distribution and dispersal.

A. G. T.

Gibbs, L. S. "A contribution to the Phytogeography and Flora of the Arfak Mountains, etc." (Dutch N.W. New Guinea.) London, Taylor & Francis, 1917. Price 12s. 6d.

Miss Gibbs prefaces her systematic account of the plants she collected in the Arfak Mountains, situated 40 or 50 miles from the east coast of the great N.W. Papuan peninsula, with a useful description of the vegetation met with during her journey from the coast.

(1) *Beach formation of the immediate shore line.* With the exception of a few mangrove swamps and sand spits at the mouths of rivers the beach is mostly narrow, very steep and formed of large lumps of coral. "Huge trees of *Barringtonia speciosa* lie prostrate or semi-prostrate over the sea. Young plants of *Pandanus* sp., *Dracæna angustifolia*, an immense *Crinum*, probably *C. macrantherum*, with giant stools of *Asplenium nidus*, no doubt displaced from the branches of the trees as they fell, crowd the ground—myriad prostrate *Barringtonia* seedlings attached by the one anchor root, all pointing seawards, bear witness to the force of the great waves retreating from their rush inland." "In many places the undergrowth is so thick or the prostrate trunks so numerous that it is easiest to walk through the surf, outside the branches of the fringing trees."

(2) *Inundation forest belt: "korang" or coral limestone zone.* "Behind the beach the low-lying belt of 'korang,' covered with forest, stretches uniformly from the coast to the foothills of the Arfak" (40 to 50 miles). This is "a sterile porous formation showing so little depth of soil that it gives the impression of walking over a reef." In 1870 Rosenberg concluded that this area is still rising and he quotes the older inhabitants as saying that they remembered low scrub where forest now stands. The rivers cut their way through alluvial deposits of mud or sand, and form great open spaces—inundation areas—sand and stones in the dry, lakes in the wet season. The entire belt is uninhabited. In the forest itself species of *Ficus*, *Macaranga* and *Artocarpus* predominate, their trunks screened by immense fronds of climbing ferns and *Epipremnopsis hugeliana*, *Raphidophora peepla*, *Philodendron* spp., *Piper forestenii*, *Pothos*, etc. Piles of the huge leaves of *Artocarpus* (1 m. by $\frac{1}{2}$ m.) accumulate under the trees to be dispersed by the floods of the rainy season. *Asplenium nidus* is abundant, but epiphytic orchids rare, and the absence of flowers and fruits striking. There is little undergrowth in the forest, sodden leaves mostly filling up the interspaces in the porous korang. The most conspicuous objects are the huge *Zanonia* capsules, the size of large pumpkins, in all stages of decay. Where there is standing water groups of Sago Palms occur, often forming swamps covering large areas. Native plantations are dotted through the forest where islands of soil accumulate or alluvial deposits have been formed by the rivers. A striking group of old *Pandanus* trees about 30 m. high was met with. Similar groups are said by the Papuans to be scattered through the forest. "These groups possibly represent the first vegetative covering of the 'korang,' displaced later by more rapidly growing dicotyledonous forest trees."

(3) *Secondary forest of the Arfak foothills* (up to 7000 feet). This is an inhabited zone with numerous *kebuns* (plantations), the ground is rocky and broken, and the forest is more varied than on the korang, both in trees and lianes, with a graceful epiphytic flora. Few species are cited by name. The cultivation consists of sweet potatoes, papaws, plantains, gourds, sugar cane, etc. with maize and tobacco as the altitude increases.

(4) *Low mountain forest above 7000 feet.* Systematic collection was limited to this formation, which is characterised by numerous conifers. The author subdivides it as follows:

(a) *Mossless Forest.* Slender straight trees 13–16 m. high with a very open, chiefly herbaceous undergrowth. **Quercus lauterbachii*, **Podocarpus papuanus* (near *P. imbricatus*)

* Endemic species.

P. rumphii (abundant), *Phyllocladus hypophyllus*, *Gleichenia linearis*, *Nephrolepis acuminata*, *Polybotrya arfakensis*, *Freycinetia gibbseæ*, *F. flaviceps*, **Alpinia domatifera*, *A. arfakensis* var. *subsessilis*.

(b) *Intermediate mossy forest.* *Dacrydium novo-guineense*, *Libocedrus arfakensis*, **Podocarpus papuanus*, *P. rumphii*, *Phyllocladus hypophyllus*, dominant, with a great variety of other smaller trees, e.g. *Drimys arfakensis*, *Spiræanthemum bellatum*, *Boeckia frutescens*, *Backhousia arfakensis*, **Idenburgia arfakensis*, **Timonius filipes*, etc. *Sphagnum novo-guineense*, *Rhacopilum spectabile*, **Dawsonia gigantea*, magnificent and abundant, with creeping *Lycopodium cernuum*, formed part of the prevailing moss carpet, from which rose abundant ground orchids including **Cryptostylis arfakensis* and *Bulbophyllum muricatum*. Among the ground ferns were *Dipteris conjugata* and *Histiopteris incisa*, and of epiphytes *Trichomanes palmatifidum*, *Hymenophyllum cinnammum*, *Lindsaya hymenophylloides*, **Polypodium remigerum*, *P. stenophyllum*, *P. clavifer*, and the orchids *Octarrhena cylindrica*, *Dendrobium glaucoviride*, *Phreatia spathulata*.

(c) *Mossy forest.* A sterile type limited to the highest point of the ridge. The prostrate and erect trunks of the small stunted trees, with the ground between, were swathed in long moss, which stood out straight from its supports, rigidly turgid. Here were *Schizæa malacana*, *Gahnia psittacorum*, *Halorrhagis suffruticosa*, *Nepenthes maxima* var. *nana*, *Trichomanes digitatum*, *Hymenophyllum cinnammum*, **Polypodium papuanum*, **P. remigerum* (the last four as epiphytes): also **Luzuriaga aspericaulis* and **Rhododendron angiense*.

These lists from the south-west ridge of the Arfaks give an idea of the vegetation of the different forest types. An even better collecting ground was an intermediate mossy forest forming a circular patch in the middle of the marsh of the lake basin. Along the edge which bounded the marsh was an *Araucaria*-forest with **Araucaria beccarii* predominant. Here *Araucaria* and *Libocedrus* seedlings were met with in all stages of growth, with *Dawsonia gigantea*, ferns, orchids, etc.

The open summit of Koebré mountain (9000 feet) between the two Angi lakes forms a flat plateau with a hard surface of disintegrated quartz granite. A remarkable association of *Cladonia* (*C. verticillata*, *C. didyma*, *C. coccifera*) spreads over the area as a uniform grey carpet about 3 cm. high. In places *Pteridium aquilinum*, var. *lanuginosum*, or *Gleichenia vulcanica*, and in damper places dense mats of *Centrolepis novo-guineensis* replaced the *Cladonias*. Among the associated plants were several endemic species. These open associations on the tops of mountains are apparently common in New Guinea, as elsewhere in the tropics, and are often at least due to repeated burnings. Miss Gibbs calls attention to the fact that what she calls "opportunity" plant associations of the Arfak mountains are made up of indigenous or even of endemic plants. This is in striking contrast to similar open spaces in other parts of the world, for instance in New Zealand and the Pacific islands, where such floras are commonly made up very largely of alien plants. The author considers that this difference furnishes evidence of the autochthonous character of the Papuan flora. Apart from the question of endemism the indigenous character of these ombrophobous "opportunity" associations would seem however to be the natural consequence of New Guinea "being a mountainous forest country...sparsely inhabited, with little or no inter-communication between the different tribes, and no migratory herds of grazing animals, there is everything to conserve and nothing to modify natural conditions." In such conditions, whatever the *history* of the native flora, one would expect the "opportunity" associations to be indigenous, just as when the reverse conditions obtain one would expect them to be largely alien.

Miss Gibbs produces much evidence that the Papuan flora may be regarded as a central stock from which the Malayan, Polynesian and Australian floras have been largely derived.

* Endemic species.

"The flora of the mountains of New Guinea, almost unknown outside the last ten years, must now be considered the axle of a wheel of distribution, of which the spokes alone have so far been familiar to us. This is in agreement with all recent work at similar or greater altitudes. Had that axle, even now barely investigated, been worked out first, we would, as a matter of course, speak of Papuan elements in neighbouring floras, as the German and Dutch botanists have already rightly suggested."

Of 330 plants the author collected in the Arfaks 100 are new to science, with one new family and five very distinct new genera. This still further emphasises the view that Papuan forms are the original stocks from which Australian, Polynesian or Malayan species are derived. The proportion of endemism is very high in the Papuan mountains as a whole, which appear to contain an immense mass of species that may well have formed the primitive stock from which offshoots have struck into Malaya, Polynesia and Australia. Schlechter's work on the orchids of eastern New Guinea and much other recent work point in the same direction. A single case out of many given by Miss Gibbs will sufficiently illustrate what is meant. *Trimenia weinmanniaefolia* Seem. was described in 1852 from Fiji. This dioecious plant remained the type of a supposed monotypic Polynesian genus, closely allied to the dioecious *Piptocalyx moorei*, ranking as a monotypic Australian genus, till Ridley in 1916 described *T. papuana* from Mount Carstensz. *T. arfakensis* is now described, as well as a new closely allied genus *Idenburgia* with a syncarpous bilocular ovary. The position of *Trimenia* and *Piptocalyx* in the apocarpous Monimiaceae is thus rendered untenable, and the new family Trimeniaceae has had to be set up to include the three genera, the majority of whose known species, shewing the most primitive forms, are thus now Papuan, the two dioecious species appearing as derived.

Unlike Mr Guppy, in the book reviewed on another page, Miss Gibbs attributes great importance to the distribution of seeds by wind over great distances, and cites corroborative evidence from the great heights to which sand grains have been found to be carried. The decisive point would seem to be the existence or otherwise of ascending air currents. To distribution by winds at high altitudes the author attributes the peopling of the Australian arid regions, where the conditions favour the production of numerous closely allied endemic species from Papuan progenitors.

A. G. T.

Carey, A. E. and Oliver, F. W. "Tidal Lands, a study of shore problems."

Pp. xiv and 284, with 29 plates and 54 figures in the text. Blackie & Son, London, Glasgow and Bombay, 1918. Price 12s. 6d. net.

"This work is primarily concerned with those problems which underlie the maintenance of coastal and riparian lands, and, as a factor in such control, the extent to which horticulture may be enlisted in the cause of conservation." It is written by a "maritime engineer" (to use the apt term suggested by the authors) and a plant ecologist in collaboration, and is a pioneer example of the practical use to which the scientific study of ecology can be applied. The fusion between the work of the two authors is not ideally complete, but the book gives a thoroughly practical, informative and suggestive account of the existing methods, the causes of their frequent failure, and the future possibilities of coast protection, and of the maintenance of harbours and waterways.

Professor Oliver is responsible for rather more than half the book, and his contributions include chapters on "The Function of Vegetation," "Sand Dunes," "The Fixation and Plant Protection of Sand Dunes," "Shingle Beaches and their Fixation," "Plant Winning of Tidal Lands—Salt Marshes," and "Blakeney Point, Norfolk, from an engineering point of view." These chapters include some of the best general accounts of the three types of

vegetation of our maritime lands hitherto published in English, and written so as to bring out the functions of the various plants in stabilising the various substrata they inhabit.

In the case of sand dunes we have a clear and full description of the technique employed with success on the Prussian, French and Australian coasts. A necessary distinction is drawn between the formation and maintenance of an adequate protective littoral dune ridge on the one hand and the fixation of inland wandering dunes on the other. The sand dune problem may be said to have been solved, and all that is wanted is the application, with suitable local modifications and improvements, of the existing technique. Not so the problems connected with shingle beaches, a subject Professor Oliver has made peculiarly his own. The descriptions of the actual function and behaviour of the various shingle-inhabiting plants are most interesting and instructive, and represent almost entirely new work during the last 10 years on the part of Professor Oliver and his colleagues. The author places his faith mainly in *Suaeda fruticosa* as the future stabiliser of shingle beaches. This plant, which is very local on the British coasts, but most abundant and vigorous where it occurs, has an astounding capacity for rejuvenation when pounded and covered by shingle, and this reaction greatly increases its stabilising powers. Nature herself, however, never completes the process of stabilisation of shingle beaches by plants, and we have to go further on the lines she points out. Excellent practical suggestions for plantation with a view to stabilising mobile shingle are given, though we do not gather that the methods suggested have been actually tried.

The account of the vegetation and development of the salt marsh is also very good, though but little practical suggestion as to control or improved utilisation is given. The case of *Spartina Townsendi* is discussed in some detail, and its unrivalled powers as a rapid landwinner are well brought out. Attention is called to the dangers of the deterioration of navigation facilities as a result of the raising of the level of tidal lands by the increase of *Spartina* and the consequent restriction of the volume of tidal water available for keeping channels free by its scouring action. The problems involved in the stabilisation of sea cliffs, and the somewhat parallel case of railway cuttings are somewhat lightly touched upon.

The necessity of a public department able to experiment and to determine on suitable courses of action in regard to all coastal problems and particularly those involving the use of vegetation is constantly insisted upon.

The style of the book is in the main well suited to its audience, though here and there the phrasing and terminology are a little heavy for those unused to the language in which scientific discussions are usually written. There are a number of excellent photographic plates and text diagrams which greatly add to the attractiveness and usefulness of the book.

A. G. T.

OBSERVATIONS ON THE ECOLOGY OF
EPILOBIUM HIRSUTUM

BY LILY BATTEN.

(With fifteen Figures in the Text.)

In the course of an investigation of the growth of the rhizome of *Epilobium hirsutum*, which had been planted in the bog-garden of the Botanical Department of the University of Bristol, material was collected from varying habitats, and it was observed that a loosely packed tissue, developed from a phellogen, was present in those plants which had been growing in the water. Scott and Wager (3), p. 312, have worked on a similar tissue in the floating roots of *Sesbania aculeata*. They considered that it came under the definition of periderm, since it arises from a phellogen, although it differs from cork in the fact that the cells are non-suberised and living. Schenck (2), p. 526, has pointed out that many shrubs and perennials growing in marshes develop in the submerged parts of the stem, or in the portions growing in wet mud, a remarkable tissue, the formation of which is directly connected with the presence of the water. In those parts of the plants which are growing in the air, or in drier soil, this tissue is replaced by cork, with which he considers it is analogous with regard to its origin, although it differs from it considerably in its form and function. Schenck gave the name "Aërenchym" to this tissue, and he found that it consisted of thin-walled non-suberised cells which have intercellular spaces of varying size, between them. He found that the spaces were filled with air, and the cells were elongated considerably in a radial direction. As a result of this elongation many of the cells have broken away from each other, so that they are not in contact over their whole surface, although a radial, and even in some instances, a concentric arrangement is visible, as in the case of cork.

The aerenchymatous cells were found by the same worker to contain protoplasm, a nucleus, and sometimes tiny leucoplasts which formed starch, while in others there was colourless cell-sap. He found that the aerenchyma, during the course of its formation, split off the layers of tissue which were outside it, in a similar manner to cork, so that the stem became eventually clothed with a secondary covering of a spongy nature, which often attained a considerable diameter. This covering was renewed centrifugally, and formed a homogeneous ventilating system, which came in direct contact with the water, but without allowing the latter to penetrate into the intercellular

spaces. Schenck's work was concerned principally with *Jussiaea*, although he discovered later that a number of marsh perennials and herbs of widely dissimilar families revealed the same phenomenon. He mentions that it occurs in *Epilobium hirsutum*, and as *Jussiaea* is a tropical type and not easily obtained in this country, while *Epilobium hirsutum* occurs in almost every county of England and Wales, it was thought that a further investigation of the aerenchymatous development in the latter would be of interest.

The anatomy of the main stem of *E. hirsutum* has been described by Solereder (4), vol. 1, p. 373. The transverse section of a young stem shows dicotyledonous bundles in a ring: the wood vessels have spiral thickening, and patches of intraxylary bast adjoin the inner margin of the wood. The endodermis is well marked, and groups of bast fibres occur in the pericycle opposite the primary bundles. In the older stem secondary thickening has taken place, and narrow medullary rays occur between the bundles. The wood-vessels are usually pitted with simple pits, although scalariform markings occur occasionally, and strengthening fibres are well developed between the vessels. The groups of bast fibres tend to elongate in a tangential direction as the stem increases in thickness, so that eventually bast fibres may occur opposite some of the secondary bundles. In the old stem the groups of intraxylary phloem are more fully developed, and the cells of both pith and cortex contain numerous starch grains. Solereder also points out that in the *Onagraceae* which inhabit marshes, aerenchyma is produced by the phellogen in place of cork.

The development of this tissue was investigated and it was found that during the latter part of the spring (the month of May in 1916 and 1917), plants of *Epilobium hirsutum* develop a phellogen which usually arises inside the groups of bast fibres (Fig. 1). If however the rhizome or shoot has not developed very fully, and no bast fibres have been formed, when the phellogen arises, the latter is produced inside the endodermis (Fig. 2). This meristematic tissue divides actively, and the nature of the cells which it produces varies in different parts of the plant. The phellogen itself presents a similar appearance to a normal cork phellogen, the cells being regular, brick-shaped and superposed. In the aerial parts of the plant, the tissue cuts off normal cork, but in those parts which are submerged in either water or mud, aerenchyma is developed. The tissue differs from cork in its loosely-packed nature, the non-suberised character of the walls, and in the fact that the cells are living. When contrasting the tissue with the aerenchyma produced under similar circumstances in *Jussiaea* Schenck (2), p. 562, points out that "bei dem ersten Typus (*E. hirsutum*) sind alle Zellen mehr weniger gleichgestaltet, radial gestreckt und nicht in regelmässige Zonen angeordnet, bei dem zweiten Typus (*Jussiaea*) dagegen baut sich das Aerenchym auf aus concentrischen, einschichtigen Zelllagen, die durch radial gestellte Zellbalken verbunden sind." Both types of aerenchyma are however produced in *Epilobium hirsutum*, and

Schenck apparently observed this fact, because he writes later: (2), p. 542, "An der Wurzel entsteht das Phellogen aus dem Pericykel und erzeugt ein Aërenchym, das verschieden von dem des Stengels aus concentrischen Lagen sich aufbaut." I have been unable to find this type of aerenchyma in the adventitious roots formed on the rhizome, but as the lower part of the upright rhizome might easily be mistaken for main root, it seems possible that Schenck may have been referring to that part of the plant. On the contrary, the tissue described may have been found in the roots of plants grown from seed, and not produced by vegetative reproduction.

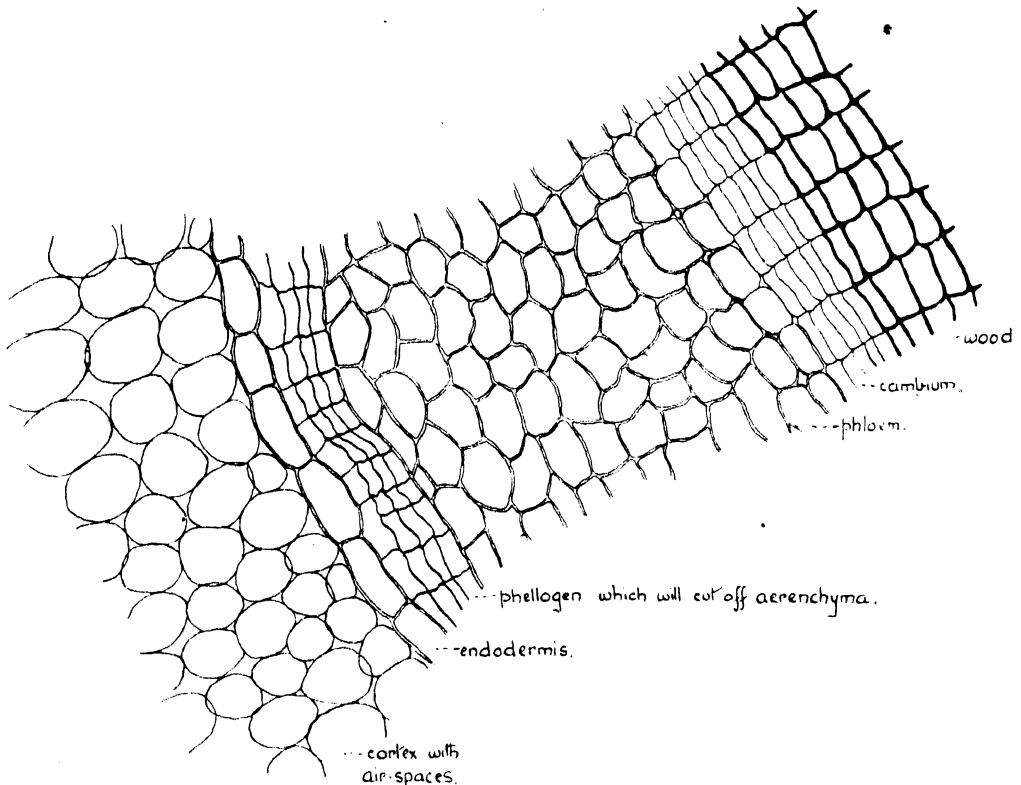


FIG. 1. T.S. of submerged portion of vegetative shoot, showing phellogen arising inside the endodermis. $\times 100$.

That part of the rhizome which is embedded in the mud is clothed during summer with a white spongy aerenchymatous covering formed by the production from the phellogen of a system of tangential plates or concentric cell-layers, with radially elongated cells acting as supports to connect the plates. In transverse section then, the tissue appears as concentric rows of cells connected by radial supports (Fig. 10). This tissue only occurs on that part of the plant which is below the mud-level, but the cells cut off by the phellogen for a short distance above the mud-level are slightly rounded off, although the number of cells produced is very much smaller (Fig. 7). During the time that

aerenchyma has been developing in the mud, the phellogen has been cutting off a few rows of cells similar in shape to cork cells, in the portion of the vegetative shoot which is submerged in water. The formation of aerenchyma in this part appears to be a subsequent development. The tissue formed in the mud is comparable to the aerenchyma described by Schenck for *Jussiaea*, although in the latter the supporting cells are radially elongated to a much greater extent. A comparison of the transverse sections of the early stages in

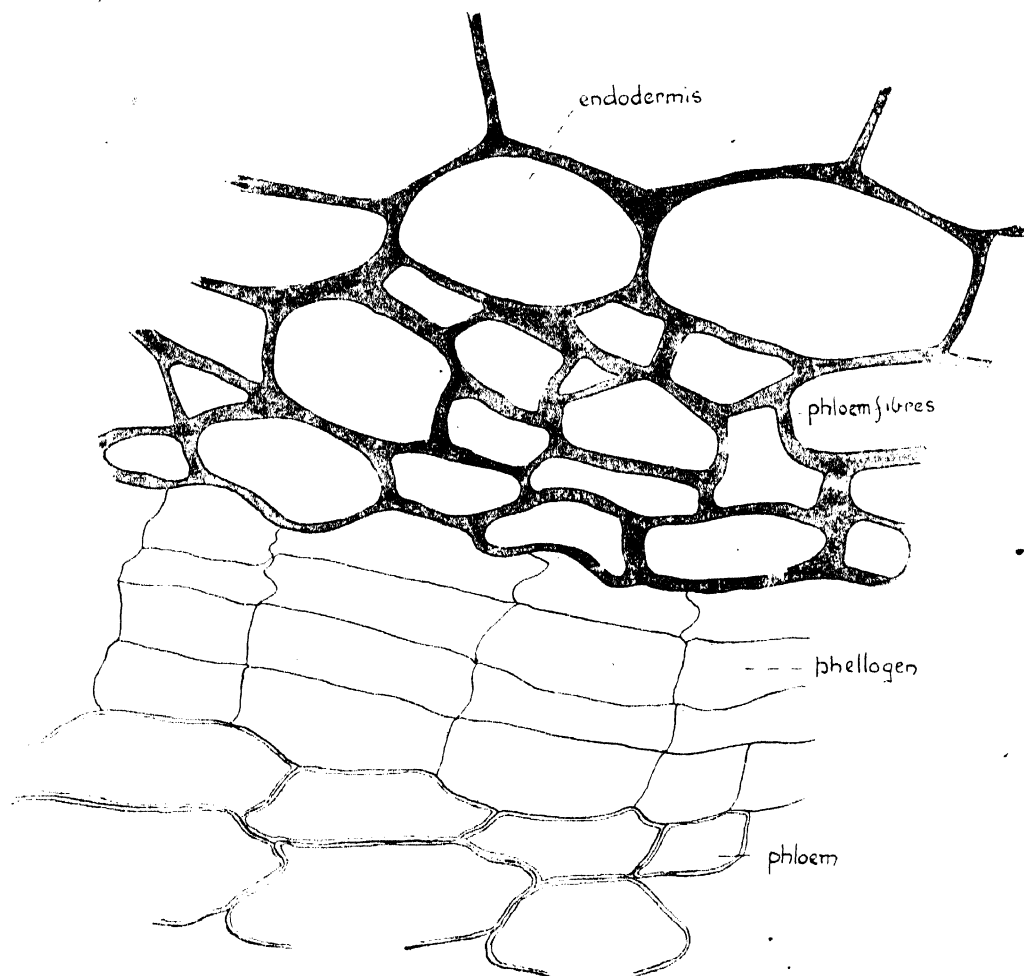


FIG. 2. T.S. of submerged portion of vegetative shoot, showing phellogen arising inside the phloem fibres. $\times 500$.

the formation of the aerenchyma of both plants shows marked similarity of form, development proceeding along the same lines in both cases, the actual extent of the elongation of the supporting cells being merely a question of degree.

Material gathered from a stream in North Somerset in October, 1916, shows a band of aerenchyma in the part of the vegetative shoot which is submerged

in water, but the tissue differs from the aerenchyma previously described, and consists of a series of radially elongated aerenchymatous cells, with large air spaces between them, but possessing no definite concentric arrangement (Fig. 4). The amount of aerenchyma developed is not uniform throughout the whole of the region which is submerged in water, but the tissue thins out towards the water-level on the upper side (Fig. 3), and is replaced by the concentric type of aerenchyma at the mud-level on the lower (Figs. 4-10). When the formation of aerenchyma begins in this area, the cells which have already been cut off by the phellogen,—simultaneously with the aerenchyma formed in the mud—become pushed outwards, and this accounts for the presence of a few rows of more or less brick-shaped cells bounding the aerenchymatous band on the outside. The remains of the primary cortex may also be seen outside the aerenchyma. It was considered at first that the brick-shaped cells belonged to an outer cork-forming phellogen, but their contents were found to give no reaction for acids belonging to the tannin group, and examination of earlier stages in the development of the tissue showed that they originated from the same phellogen as the aerenchymatous tissue.

The phellogen layer is thus capable of cutting off different types of tissue, which vary as the nature of the surrounding medium. Response apparently occurs most readily in that part of the rhizome which is growing in the mud. The phellogen at first cuts off brick-shaped cells which are not suberised in the portion growing in the water, but it subsequently develops aerenchyma, which is different in form from the tissue produced in the mud. In the latter case, the product of the phellogen is definite aerenchyma from the earliest stage of development.

Material which has not been submerged in either water or wet mud shows no development of aerenchymatous tissue, and it appears therefore that its formation is a direct response to external conditions of life. An experiment was set up to ascertain whether change of environment would be accompanied by immediate response, and for this purpose young rhizomes were gathered on 15. xi. 1916, and their environment was changed as follows:

A. Rhizomes from a sandy bank were planted in mud and submerged in water.

B. Rhizomes from a stream were planted in a pot of soil from the sandy bank. Controls were kept of both experiments, and on May 16th, 1917, the plants were examined.

A. The part of the rhizome which was submerged in mud had developed a white spongy covering of aerenchymatous tissue, tangential plates with radially elongated chains of supportive cells. The part of the rhizome which was submerged in water had developed a phellogen, and a few layers of brick-shaped cells had been produced, but aerenchyma had not yet been formed. A later examination, however, showed that aerenchyma of the irregular type was developed in this region.

B. Although the plant had been grown in comparatively dry soil, a

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definite band of aerenchyma had been produced in the part of the rhizome below the soil level, but no aerenchyma was formed by the portion of the shoot above the soil.

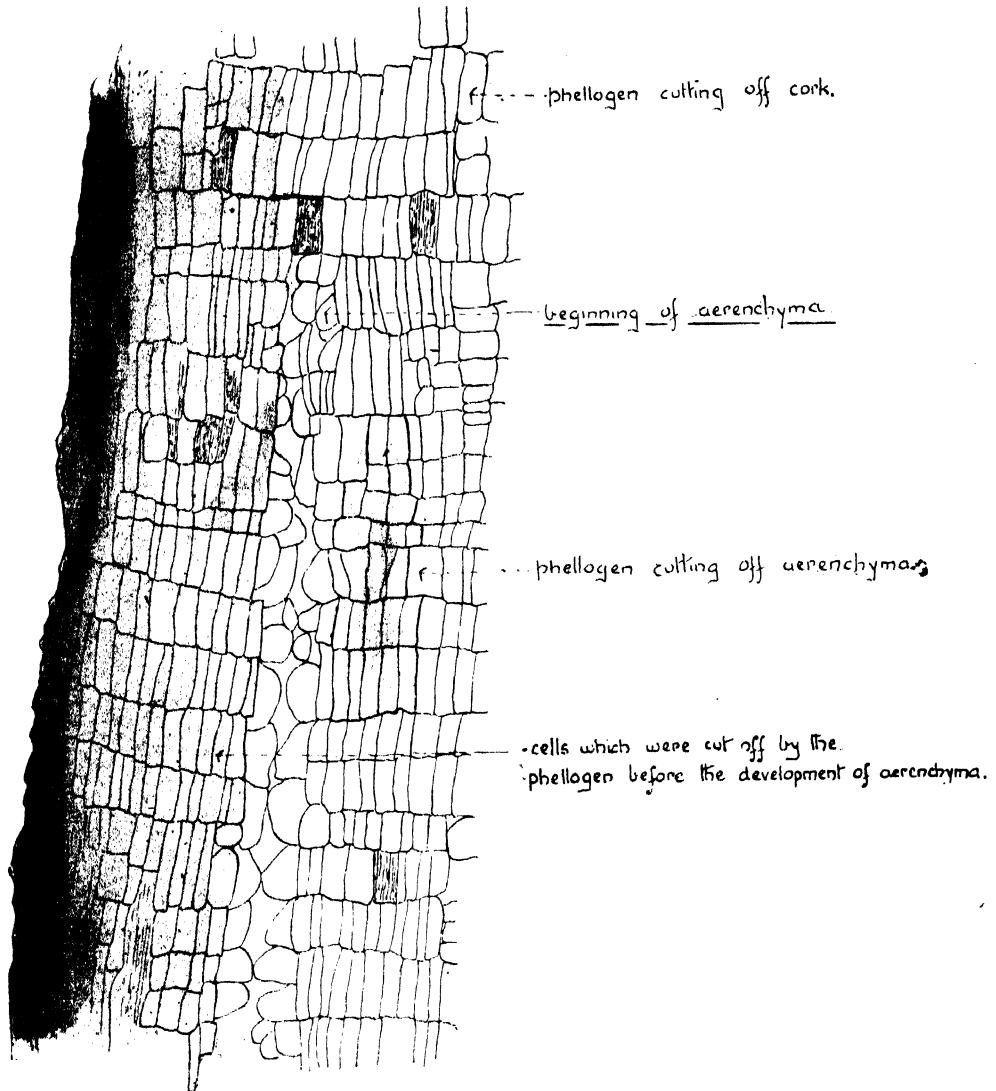


FIG. 3. L.S. of outer layers of main stem showing thinning out of aerenchyma at the water-level. $\times 100$.

Aerenchyma is produced therefore in *Epilobium hirsutum* as a definite response to external conditions. The presence of mud produces a quicker response from the plant than the presence of water. Response takes place rapidly, and occurs during *one vegetative season*, in a plant that has been moved from a dry habitat into a wet one. The plant however which was moved from water into sandy soil responded much less readily. This may be understood, because the plant *A* would have been unable to get enough oxygen for growth,

unless it developed aerenchyma, while immediate adaptation was not essential to the life of *B*.

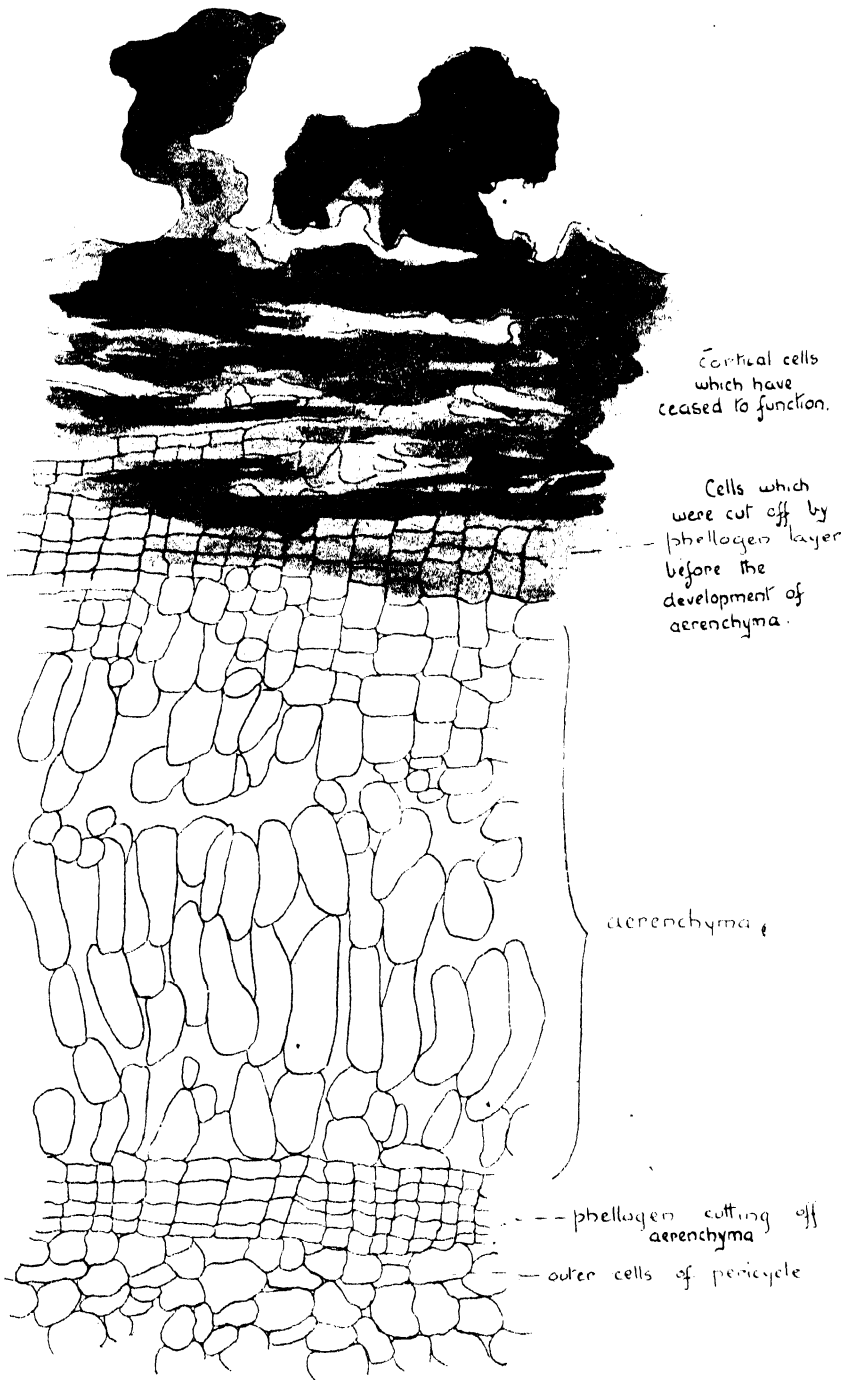


FIG. 4. T.S. of outer layers of main axis, showing maximum development of aerenchyma (with no concentric arrangement) in the portion of the shoot which is submerged in water. $\times 120$.

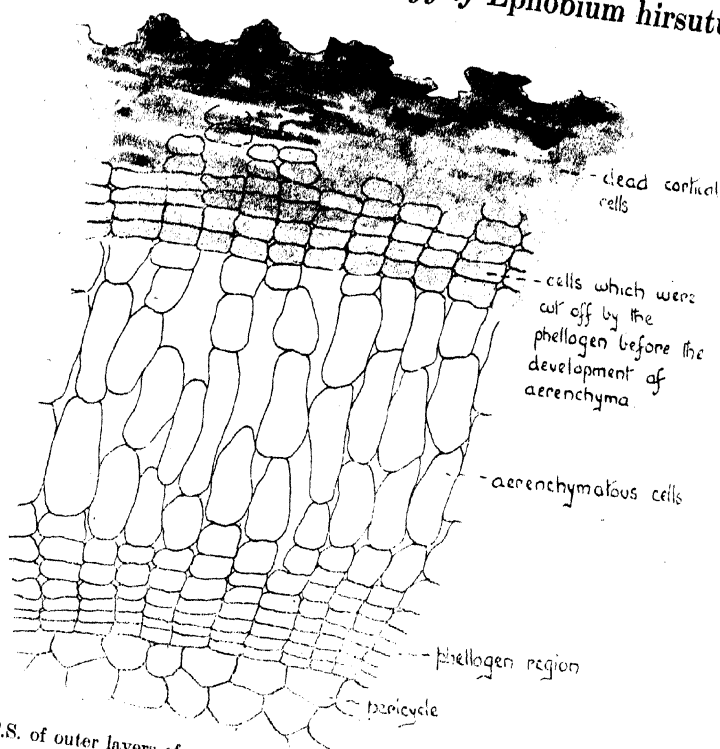


Fig. 5. T.S. of outer layers of main axis, nearer the mud-level than Fig. 4. Aerenchyma less developed. $\times 120$.



Fig. 6. T.S. of outer layers of main axis, nearer the mud-level than Fig. 5. Very little aerenchymatous development. $\times 120$.

In the adventitious roots, I have been unable to find any aerenchyma, the phellogen in this case cutting off layers of cells with brown contents, alternating with layers having little or no contents (Figs. 11-13). These colourless cells may perhaps be analogous with the "phelloid" cells described by Von Höhnelt, and

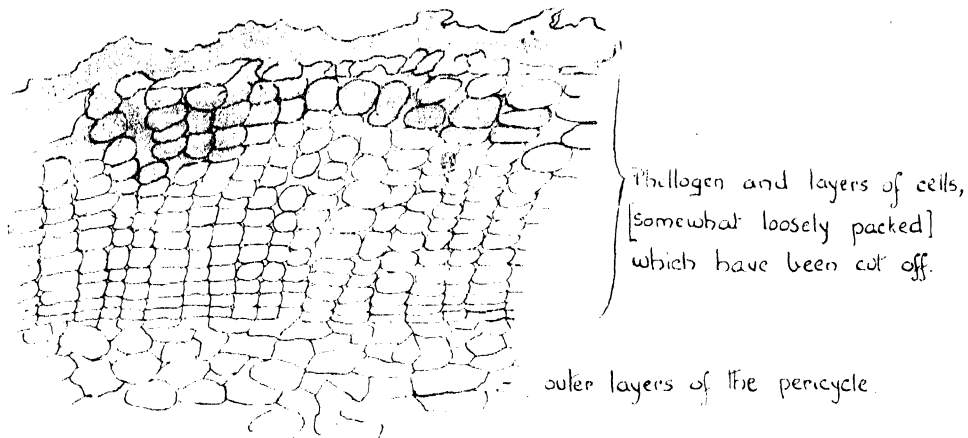


FIG. 7. T.S. of outer layers of main axis, very near mud-level. No aerenchyma of type shown in Figs 4-6 is present, but cells show signs of rounding off, suggesting the early stage of the "mud" type of aerenchymatous tissue. $\times 120$.

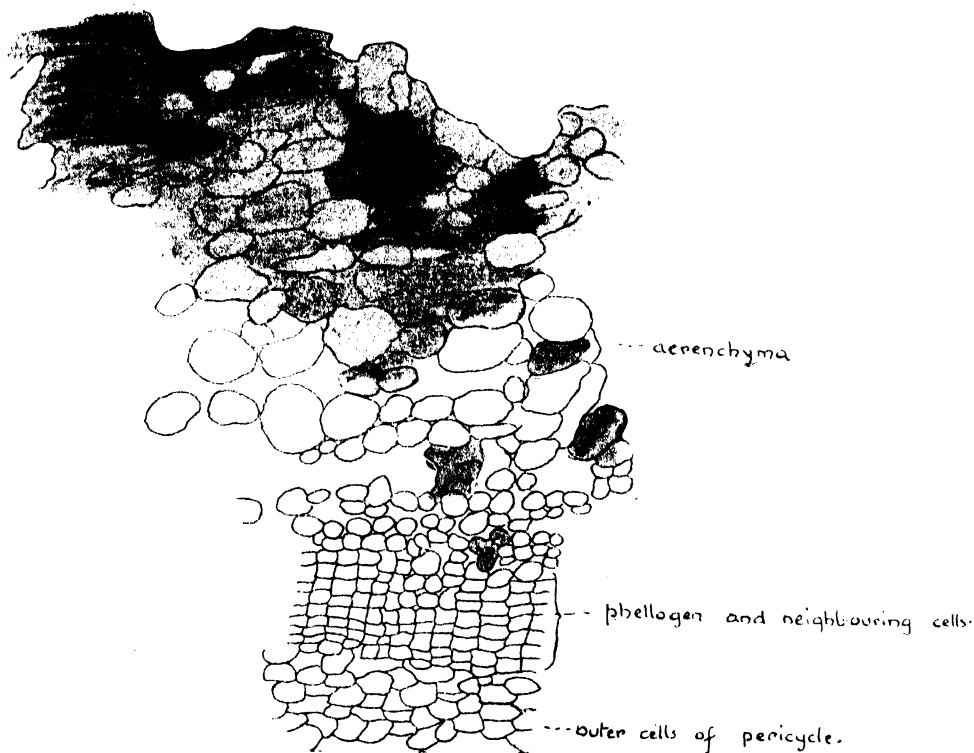


FIG. 8. T.S. of outer layers of main axis, at the mud-level. Aerenchyma has been formed, and is beginning to show signs of concentric arrangement. $\times 120$.

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referred to by Schenck (2), p. 526, viz.: "Das Periderm gliedert sich von innen nach aussen gerechnet in Phelloderm, Phellogen und Kork, welch' letzterer nach den eingehenden Untersuchungen von Höhnel's nicht immer aus lauter verkorkten Zelllagen besteht, sondern in manchen Fällen zwischen

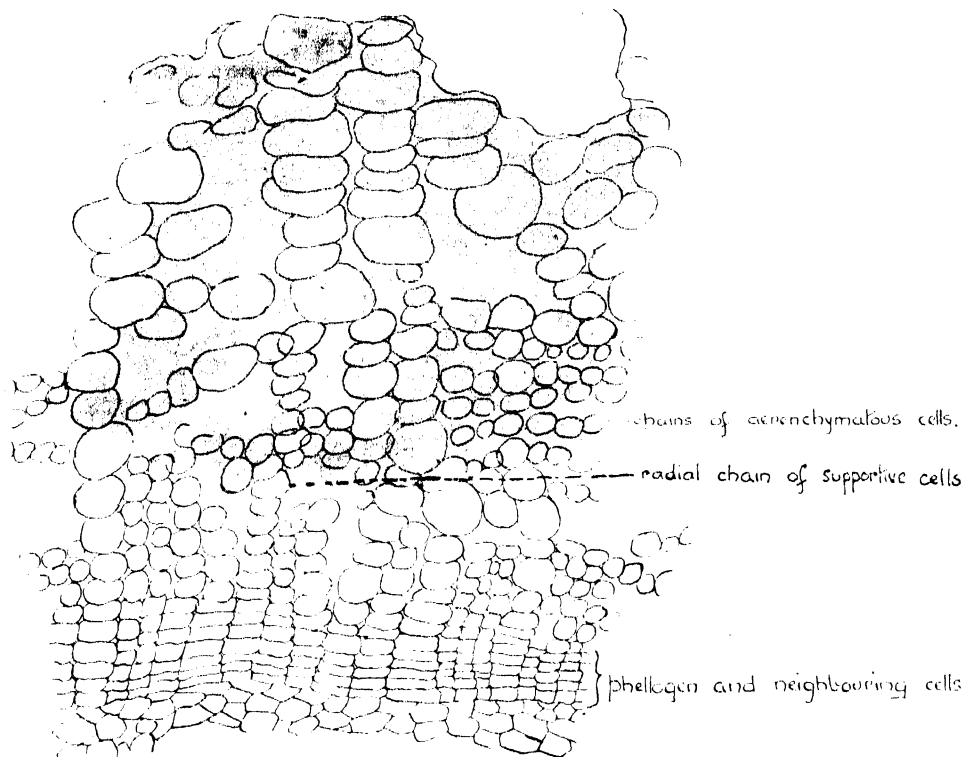


FIG. 9. T.S. of outer layers of main axis, from portion growing in the mud. Shows concentric arrangement of aerenchyma. $\times 120$.

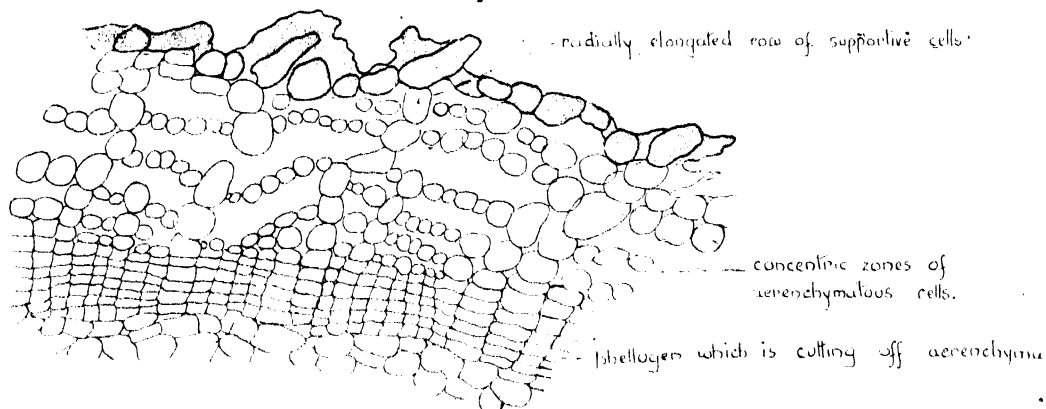


FIG. 10. T.S. of outer layers of main axis, showing complete development of tangential plates, with radial chains of supportive cells between the plates. $\times 90$.

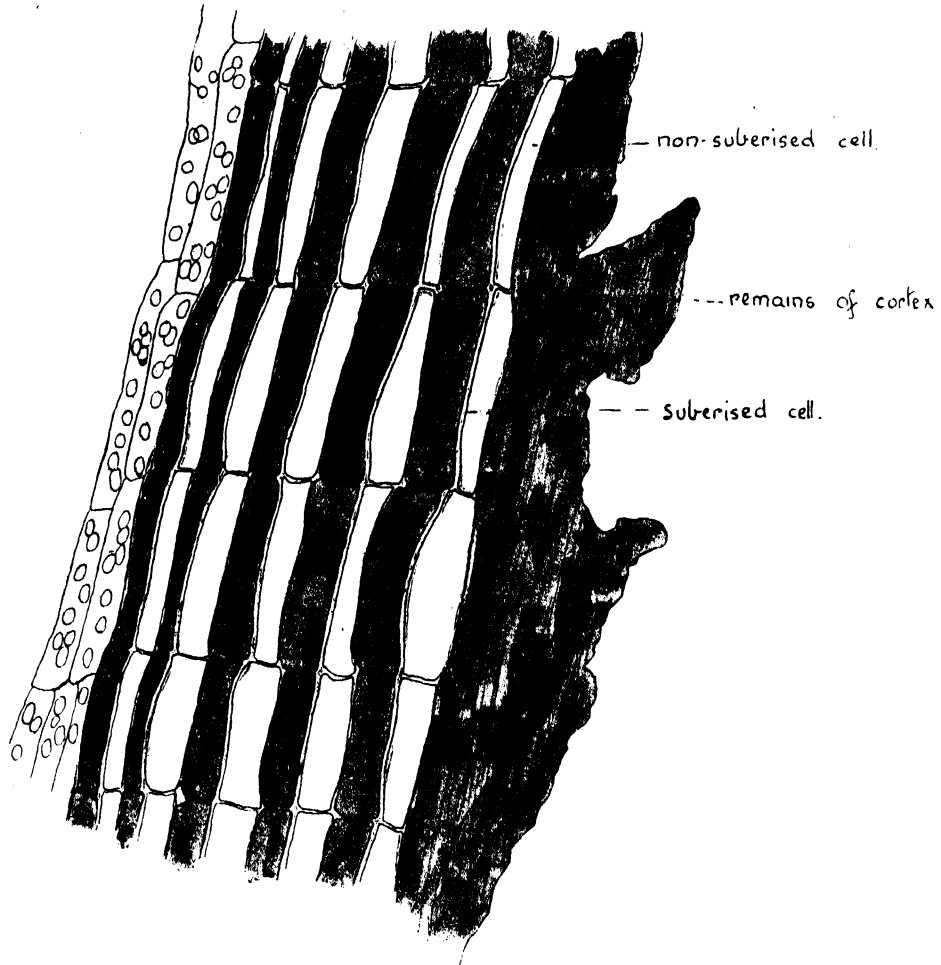


FIG. 11. L.S. of lateral root, showing alternating layers of suberised and non-suberised cells. $\times 330$.

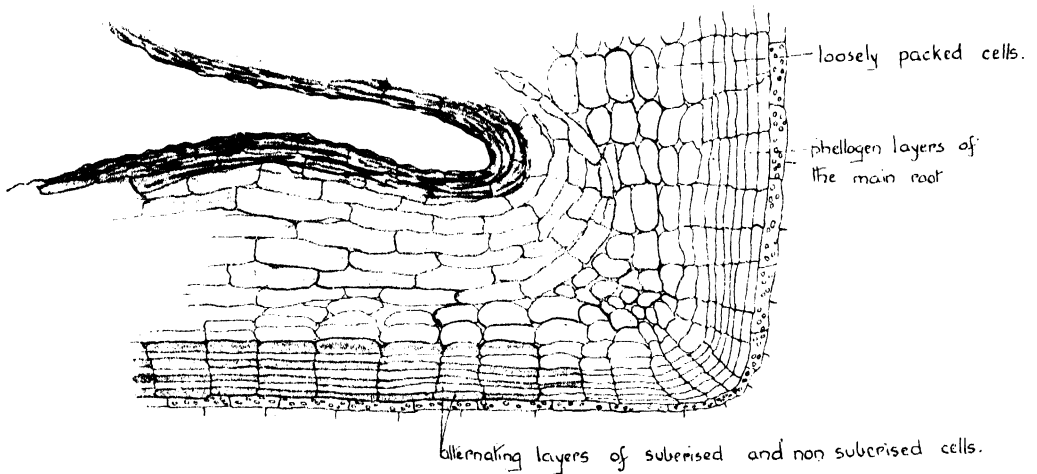


FIG. 12. L.S. through junction of rhizome and adventitious root, showing phellogen region, and transition from loosely packed cells in the rhizome, to alternating layers of phelloid and non-phelloid cells in the lateral root. $\times 100$.

den verkorkten Lagen auch solche ohne jegliche Spur von Korkstoff enthält." Solereder (4), vol. II, p. 932, also mentions that: "in many members of the order (*Onagrarieae*) the tissue of the cork includes both suberised and unsuberised (phelloid) cells, and in some cases (species of *Fuchsia*), there is a regular alternation of layers of cork-cells and phelloid cells."

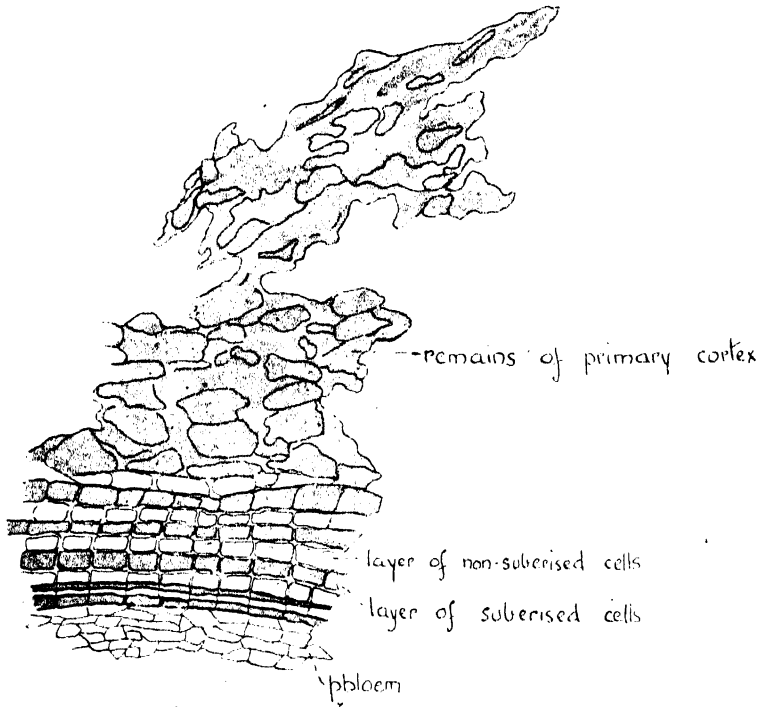


FIG. 13. T.S. of portion of lateral root, from material growing in the water, showing alternating layers of suberised and non-suberised cells. $\times 120$.

In the young root of *Epilobium hirsutum*, the cells of the cortex are very loosely packed, and large air-spaces occur in the roots of plants grown under very moist conditions (Fig. 14). In *Jussiaea*, Schenck has described the aerenchyma in the aerotropic roots as being developed from the primary cortex (2), p. 533, but in that case the tissue is of such distinct form as to merit the use of the term "aerenchyma." In *Epilobium hirsutum*, however, it appears to be a loose cortical tissue, rather than definite aerenchyma.

In the cortex of the young root, isolated cells occur with dark-brown contents. The brown substance belongs to the tannin group, as may be shown microscopically in the following ways: A drop of dilute solution of iodine $n/100$ in potassium iodide, when placed on the section, causes a pale pink coloration. The brown substance changes to greenish yellow, when tested with baryta water.

In order to test the effect of growing plants in different soils, seeds which

had been produced by plants growing in running water were sown in pots containing respectively (a) clay and (b) sand.

The seeds germinated readily in each pot, but the green shoots of those grown in clay developed more rapidly than those grown in sand, although the root-systems of the former were smaller, the rootlets being fewer and shorter than in the sand-grown seedlings (Fig. 15). A comparison of the transverse sections of the roots shows much larger air-spaces in the plants grown in clay. This is comparable with the result obtained by Norris (1), p. 134, when growing *Zea Mais* under similar conditions.

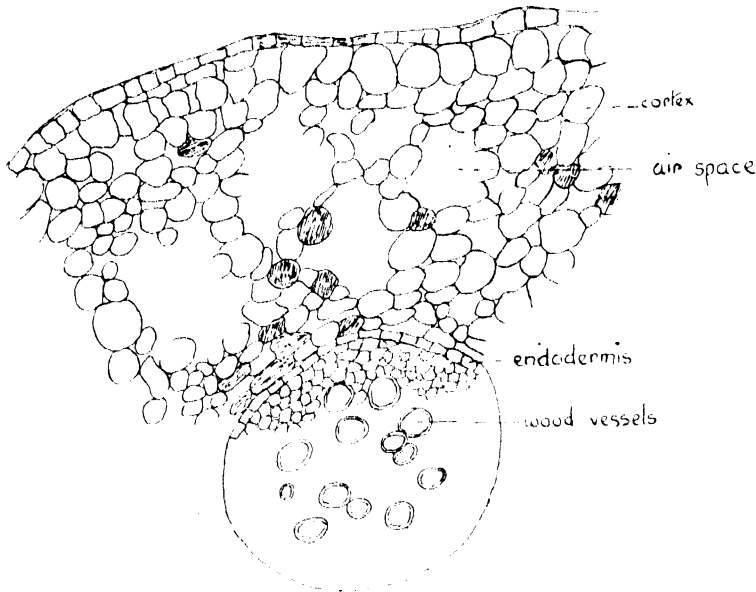


FIG. 14. T.S. of lateral root showing primary cortex with large air-spaces and cells containing a substance belonging to the tannin group. $\times 120$.

During the month of September, sections were cut just below the soil level, in order to ascertain whether there was any trace of aerenchymatous development in these plants, as a result of the parent having grown in water. Examination showed however, that neither clay nor sand-grown seedlings had developed any aerenchymatous cells, confirming the view that the presence or absence of that tissue is a direct adaptation of the individual to its environment.

With regard to the function of the aerenchymatous tissue, Schenck (2), p. 562, states that the air stored in the lacunar spaces has been tested by Dr Immendorff, and found to be 30 per cent. richer in O than atmospheric air, and to contain a considerable quantity of CO_2 in addition to O and N. It is evident therefore that the tissue facilitates the supply of O to those parts of the plant which are immersed in either water or mud, and consequently are but little exposed to atmospheric air.

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Scott and Wager (3), p. 312, have described the formation of aerenchyma in the floating roots of *Sesbania aculeata*, and they termed it "floating tissue." In *Epilobium hirsutum* however, the aerenchyma does not appear to function as a floating-tissue, since the main rhizome is fixed in the mud, and although adventitious roots, which may float in the water, arise up the stem, I have not found any definite aerenchymatous development in these laterals, although the cells cut off by the phellogen are in some cases slightly rounded off.

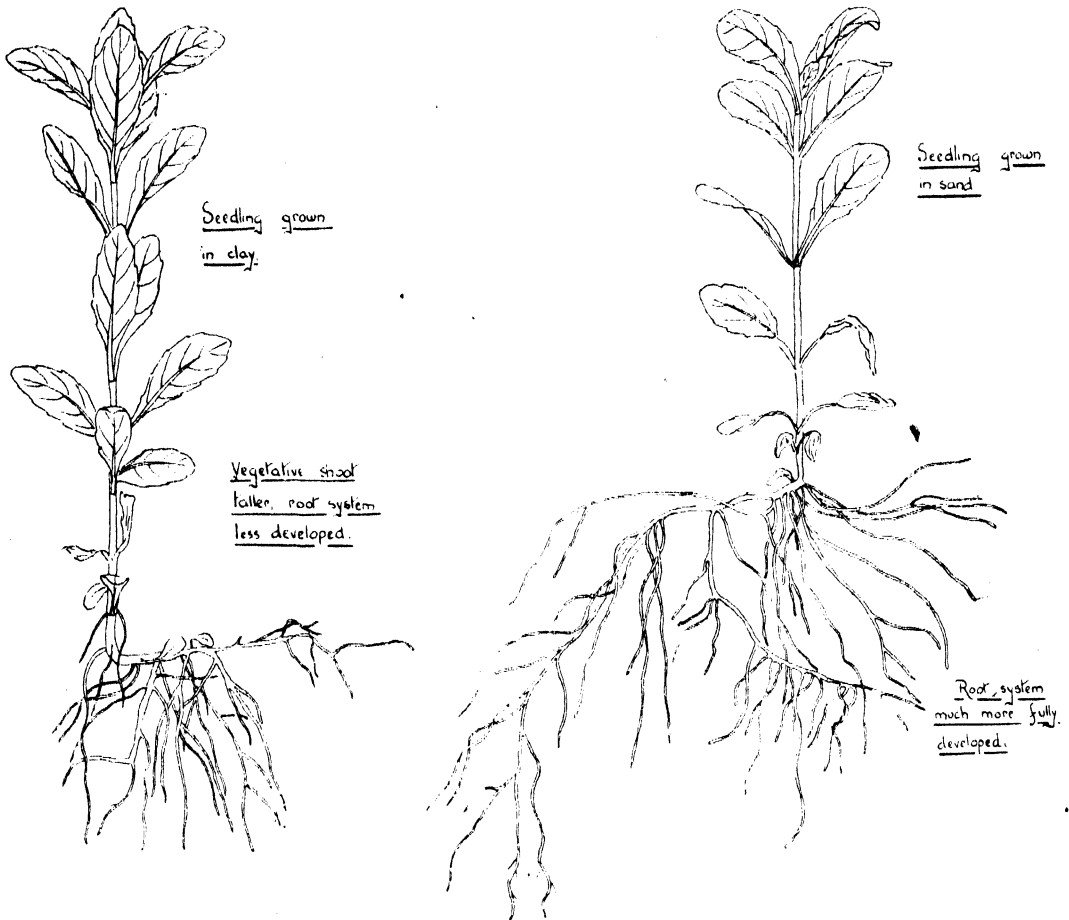


FIG. 15. Comparison of seedlings grown in clay and sand respectively. $\frac{1}{3}$ nat. size.

The external character of the rhizome varies in appearance according to the nature of the surrounding medium. If the plant is growing either in very wet soil or submerged in water, the rhizome is succulent, and the root development is very considerable, a large number of adventitious roots being developed. When, however, the soil is comparatively dry, or of a sandy nature, and consequently physiologically dry, the rhizome is much less fleshy, and the roots are fewer.

An experiment was set up in order to ascertain whether the presence of water influenced the direction of growth of the rhizomes, but it was found that the young rhizomes which were formed by the plant grew out in all directions, irrespective of the relative situation of the water.

The following experiment was carried out to ascertain whether seeds of *E. hirsutum* will germinate when grown below the water level in slowly changing water.

Apparatus was set up, by means of which water was kept constantly dripping from a higher vessel into a glass dish which contained a perforated porcelain vessel. The seeds were enclosed in the porcelain pot which was lined with muslin. The water in the vessel containing the seeds was thus kept slowly changing.

The result of the experiment was that by the end of a fortnight the seeds had begun to germinate, and radicles were well developed. The experiment was allowed to remain, and growth continued slowly, but the seedlings were weakly, the internodes being considerably elongated, while the leaves were much reduced.

Examination of the anatomy showed very little development of wood, but the air-spaces between the cortical cells were not as large as might have been expected. This is probably due to the fact that a certain amount of air was available for the plant in the slowly changing water.

It was found therefore that the seeds will germinate below the water-level, provided that the water is slowly changing.

An experiment was set up to ascertain whether seeds will germinate below the water-level, and also in which position relative to the water-level they germinate best, when the water is stagnant.

A constant level of the water was maintained by means of a siphon, and an inverted bottle with a glass tube fixed into the cork. The inverted bottle was filled with water, and the edge of the glass tube reached the water-level in the beaker below. This kept the water-level constant in the beaker, and a siphon passing from the beaker to the glass vessel in which the seeds were placed kept the level constant there. Some of the seeds were fastened to a porous plate with wax, while others floated in the water. As the amount of water added was only equal to the amount lost by evaporation, the water in the vessel containing the seeds was practically stagnant.

The result of this experiment was that at the end of ten days (November 27th), several seeds near the water's edge had germinated. Three days later, the radicles were visible of seeds on the porous plate, two and four cms. respectively above the water-level. Germination was not however rapid under these conditions, and it was not until January 14th, that is, nearly two months after the experiment had been set up, that growth had really begun in the majority of the seeds. At the beginning of May, the seedlings below the water-level, or floating on the water, were alive, but were very weakly, while those

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plants above the water-level had died, unless the roots could reach the water, and thus obtain sufficient moisture.

The anatomy of the seedlings grown below the water-level showed that a very small stele was present, with very little wood or bast. Air spaces occurred between the cells, and the cortical cells were large compared with the radius of the stem or root.

Seeds of *E. hirsutum* will germinate therefore below the water-level, even when the water is stagnant. Growth is more active however when the seeds are floating, although even then the plants are weakly, and the amount of moisture which is available from a porous plate is insufficient to enable the young plants to thrive.

SUMMARY.

In the early spring, plants of *Epilobium hirsutum* develop a phellogen layer which is capable of producing cork, concentric layers of aerenchyma, loose aerenchymatous cells with no concentric arrangement, or alternating layers of phelloid and non-phelloid cells, depending on the environment of the plant, and the position of the organ concerned. Material which was changed from a dry habitat to a wet one responded during one vegetative season and developed aerenchyma both in the parts growing in the mud, and also in the part growing in the water. A rhizome which had been moved from a wet to a dry habitat responded less readily to the change of environment, and produced concentric layers of aerenchyma in the part of the shoot below the soil level, although its formation was no longer essential to the life of the plant.

Seeds from a plant grown in water were planted in sand and clay respectively, but no trace of aerenchyma appeared, confirming the view that its formation is a response by the individual to an external stimulus.

Seedling experiments were carried out and it was found that the seeds would grow below the water-level, although the seedlings were weakly, but if the seeds germinated in a place where little water was available, they soon died, the moisture obtainable through a porous plate being insufficient.

CONCLUSION.

Plants of *E. hirsutum* are capable of responding to an external stimulus and adapting themselves very rapidly to the medium in which they are growing. This adaptation is effected principally by the activity of a phellogen layer, and the action of the stimulus and the response may occur during the life of one individual. The presence of water-saturated mud causes a quicker response than the presence of water alone, while a plant changed from a dry habitat to a wet one develops aerenchyma more rapidly than it loses the power to produce the tissue when its presence has become immaterial through change of environment.

This work has been carried on under the supervision of Dr O. V. Darbishire, and I should like to express my thanks both to him and to Miss E. M. Lee, M.Sc., for their helpful direction and advice. I am also indebted to Professor Vines for kind permission to use the Library of the Botanic Gardens, Oxford, and to Dr Church and Dr Hallam for supplying some of the material used.

DEPARTMENT OF BOTANY,
UNIVERSITY OF BRISTOL.

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SOME RECORDS OF THE SEASONAL FLORA OF ARABLE LAND UNDER CULTIVATION

BY L. F. NEWMAN AND R. W. NEWMAN.

For several years the writers have kept accurate records of the numerical and seasonal occurrence of the weeds of arable land under ordinary culture.

The flora of any arable field is exceedingly scanty both as regards number and species, rarely more than 30-35 species commonly occurring on a farm lying over a single geological outcrop, that is, with only one fairly uniform type of soil. Special clay, sand, loam or chalk plant-associations develop according to the character of the soil, and by reason of the agricultural operations carried out through the year these associations are composed almost entirely of annuals, with seedlings and young plants of those perennials which have wind-borne fruits capable of rapid germination; such species form the first vegetation on waste land when abandoned by the farmer.

The frequency of occurrence of arable land weeds and the flora types met with on different geological horizons have been worked out by Dr Winifred Brenchley¹ who, however, only observed the relative frequency of summer flowering plants in growing crops without reference to their actual number and seasonal distribution. Plant counts of old pastures have been carefully made by S. F. Armstrong² and others, but again only for special areas and in the summer. Seasonal records of arable land plants have also been recorded for certain western pastures and arable by R. G. Stapledon³ who counted the plants in several small areas (one sq. foot) at intervals throughout the year, the squares being selected haphazard from different parts of the same field and the counts added together.

None of these methods, however, gives an idea of the number of plants surviving ordinary agricultural operations on arable land throughout the season, and the authors therefore arranged an experiment to determine the succession of plants on one plot of land over an entire year. Their method was as follows: A square wooden frame with an inside area of one yard was thrown down in a field at a fixed distance (two chains) from the headlands. The exact site was noted by measuring coordinates to pegs fixed in the hedgerows at right angles to the sides of the frame. Pegs were thrust down nearly flush with the ground at each corner and left there when the frame was lifted up so that it could be easily slipped back on the same place at the subsequent visits. The

¹ Brenchley, *Annals of Botany*, January 1913 and 1911.

² Armstrong, *Journal of Agric. Sci.* 2, Part 3.

³ Bull. Cirencester Agric. Coll. 1912.

site was at first marked with a flag, but this was subsequently abandoned as the pole attracted rabbits, whose droppings affected the vegetation both by quickening germination and by sowing seeds of alien plants¹. In this way the same area could be examined throughout the year and the plants in the frame easily counted, sliding bars sub-dividing the space being used to ensure accuracy. The ordinary agricultural operations of the farm were not interfered with and one of us (R. W. N.) supervised the work and saw that the plots received exactly the same treatment as the rest of the field.

The tables appended show the number and species of the weeds on six such areas on fields under different crops and taken at intervals throughout the year. The plots were counted once during each of the winter, and twice during each of the summer months when the crops and weeds were growing rapidly. The farm is situated on the borders of Hertfordshire and Essex, and the soil is derived from the heavy calcareous boulder clay which covers most of the district; an average mechanical analysis being:

TABLE I.

Fine gravel	1.5 %
Coarse sand	17.0
Fine sand	17.0
Coarse silt	17.0
Fine silt	10.0
Clay	19.0
Loss on ignition	10.0
Moisture	4.0
Calcium carbonate	4.5

The rotation of each plot was:

TABLE II.

Plot	Crop	Crop taken the previous year	Crop taken two years previously
I	Clover	Wheat	Mangolds
II	Sainfoin	Sainfoin	Sainfoin
III	Oats	Wheat	Clover
IV	Wheat	Bare fallow	Wheat
V	Barley	Wheat	Clover
VI	Wheat	Mangolds	Barley

Plot II on poor undrained soil was very foul after three years' sainfoin. It was ploughed and well cleaned. The first ploughing was in April, and as the land was under a cleaning fallow for the season and gave blank records the readings were discontinued.

Plots were originally taken on potatoes and on roots, but spring tillage and rigorous hoeing throughout the season so interfered with the natural plant growth on the plots by uprooting and carrying on to them alien seedlings and young plants that they were also abandoned.

Plot VI was deliberately seated over a small patch of *Agropyrum repens* in order to ascertain how far the growth of individual shoots could be distinguished throughout the season.

¹ Lubbock, *Seeds and fruits*. Warming, *Oecology of Plants*.

Some difficulty was experienced in distinguishing a few of the plants in the cotyledon stage and similar seedlings outside the plot were pegged and visited at intervals until either the identification was confirmed or the species was recognised correctly. The authors are indebted to Professor Biffen of Cambridge for assistance in identification of some of the doubtful species. *Plantago media* and *P. major* were grouped together. No attempt was made to distinguish between the various species of *Hieracium*, and *Sonchus* was included with them. Where several of the seedlings were found in the cotyledon stage at one reading the letter C is placed after the number of plants in that stage and the figures should be added together to give the total number of individuals of the species on the plot.

The readings varied very much from one another in the different plots throughout the season, the flora of each field being quite distinct. In no case were the plots separated by more than 400 yards from each other.

The following record shows the differences in the plots on April 16.

Plot I, clover: *Cnicus arvensis*, *Lychnis vespertina*, *Medicago sativa*, *Plantago lanceolata*, *P. media*, *Scabiosa succisa*, *Tussilago Farfara*, *Veronica agrestis*, *V. Buxbaumii*.

Plot II, sainfoin: *Brassica sinapis*, *Cerastium vulgatum*, *Cnicus arvensis*, *Galium aparine*, *Linaria minor*, *Lychnis dioica*, *L. vespertina*, *Medicago lupulina*, *Potentilla reptans*, *Prunella vulgaris*, *Ranunculus arvensis*, *R. repens*, *Senecio vulgaris*, *Sonchus arvensis*, *Taraxacum officinale*, *Tussilago Farfara*, *Veronica Buxbaumii*.

Plot III, oats: *Lychnis vespertina*.

Plot IV, wheat: *Brassica sinapis*, *Cerastium vulgatum*, *Galium aparine*, *Ranunculus arvensis*, *Scandix pecten Veneris*, *Veronica Buxbaumii*, *V. agrestis*.

Plot V, barley: *Agropyrum repens*, *Brassica sinapis*, *Veronica Buxbaumii*.

Plot VI, wheat: *Agropyrum repens*, *Brassica sinapis*, *Cnicus arvensis*, *Veronica Buxbaumii*.

The agricultural operations were, owing to the nature of the crops on the plots, comparatively few in number but drastic in their effects on the weed floras.

TABLE III.

Date	I Clover	II Sainfoin	III Oats	IV Wheat	V Barley	VI Wheat
Jan. 1-30	---	---	---	---	---	---
Feb. 1-28	---	---	---	---	---	---
March 1-30	---	---	Harrowed	---	---	---
April 1-16	---	---	Drilled	---	Harrowed	---
" 17-30	---	---	---	Drilled clover	Drilled barley	---
May 1-15	---	Ploughed	---	---	---	---
" 16-31	---	---	---	---	---	---
June 1-15	---	---	Horsehoed	---	Handhoed	---
" 16-30	Cut	---	---	---	---	---
July 1-15	---	---	---	---	---	---
" 16-31	---	---	---	---	---	---
Aug. 1-14	---	---	---	---	---	---
" 15-31	---	---	Cut	Cut	Cut	Cut

TABLE III (*continued*).

Date	I Clover	II Sainfoin	III Oats	IV Wheat	V Barley	VI Wheat
Sept. 1-16	Cut	—	Sheep fed 3 days	—	Sheep fed 1 day	—
„ 17-30	Sheep fed 4 days	—	Ploughed	—	—	—
Oct. 1-31	Ploughed	—	Harrowed Drilled	—	—	—
Nov. 1-30	—	—	New crop	—	—	—
Dec. 1-31	—	—	—	—	—	—

Tillage and cleaning work generally are carried out on this type of land during the years of roots and beans or bare fallow and very little attention is given to weeds in cereal crops. The autumn ploughings account for most of them.

The following is a list of the species identified in the plots during the year—forty-two in all:

TABLE IV.

Agropyrum repens	Mentha arvensis
Anagallis arvensis	Plantago lanceolata
Brassica sinapis	P. media et major
Centaurea nigra	Polygonum aviculare
Cerastium arvensis	P. convolvulus
C. vulgatum	Potentilla reptans
Chenopodium album	Prunella vulgaris
Cnicus arvensis	Ranunculus arvensis
Convolvulus arvensis	R. repens
Euphorbia exigua	Rubus caesius
Galium aparine	Rumex crispus
Geranium dissectum	Scabiosa succisa
Hieracium sp. et Sonchus	Scandix pecten Veneris
Lamium purpureum	Senecio vulgaris
Lapsana communis	Silene inflata
Linaria minor	Taraxacum officinale
L. spuria	Tussilago Farfara
Lychnis dioica	Veronica agrestis
L. vespertina	V. Buxbaumii
Medicago lupulina	Viola tricolor

TABLE V.

Rainfall for the year 1911 (by kindness of Dr Mill).

“British Rainfall Organization.”

Record from station near to plots.

Monthly rainfall in inches.

Jan.	...	1.64	Brought forward	9.94
Feb.	...	1.16	July	...
March	...	2.08	August	...
April	...	0.88	Sept.	...
May	...	1.53	Oct.	...
June	...	2.65	Nov.	...
			Dec.	...
Forward	...	9.94		4.60
Total for year		23.13

The second half of the summer was very hot with very low rainfall in July and August.

[illegible]

PLOT II. *Sainfoin*.

	Jan. 30	Feb. 28	Mar. 30	April 16	" 30
<i>Brassica sinapis</i>	—	1	4C	9	—
<i>Cerastium arvense</i>	2	1	—	—	—
<i>Cerastium vulgatum</i>	7	2	3	2	2
<i>Cnicus arvensis</i>	4	4	2	1	4
<i>Galium aparine</i>	—	4	7	7	4
<i>Hieracium</i> sp. et <i>Sonchus</i> arvensis	—	46	52	73	75
<i>Lamium purpureum</i>	1	1	—	—	—
<i>Linaria minor</i>	—	—	1	2	—
<i>Lychnis dioica</i>	—	—	—	3	2
<i>Lychnis vespertina</i>	—	7	4	8	4
<i>Medicago lupulina</i>	2	—	5	1	1
<i>Plantago major et media</i>	2	2	—	—	4
<i>Potentilla reptans</i>	—	—	4	4	3
<i>Prunella vulgaris</i>	—	—	1	1	1
<i>Ranunculus arvensis</i>	—	—	—	1	3
<i>Ranunculus repens</i>	58	58	57	54	54
<i>Senecio vulgaris</i>	4	5	1	2	2
<i>Taraxacum officinale</i>	1	6	4	5	5
<i>Tussilago Farfara</i>	—	—	1	3	8
<i>Veronica Buxbaumii</i>	—	—	—	3	—

Ploughed and readings discontinued

PLOT IV. *Wheat.*

	Jan. 30	Feb. 28	Mar. 30	April 16	" 17-30	" 30	May 15	" 29	June 15	" 30	July 15	" 30	Aug. 14	" 15-29	Sept. 16	" 30	Oct. 31	Nov. 30	Dec. 30
<i>Agropyrum repens</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
<i>Anagallis arvensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Brassica sinapis</i>	—	11C	7	3	—	1	1	1	3	1	—	—	—	—	—	—	—	—	—
<i>Centaurea nigra</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cerastium arvense</i>	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cerastium vulgatum</i>	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	10	—	—
<i>Chenopodium album</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Convolvulus arvensis</i>	—	—	—	—	—	—	—	1	1	1	3	2	4	5	—	—	—	—	—
<i>Euphorbia exigua</i>	—	—	—	—	—	—	—	1	1	3	12	4	—	—	—	—	—	—	—
<i>Galium aparine</i>	—	—	—	2	—	2	5	5	1	2	4	—	—	—	—	—	—	4	—
<i>Geranium dissectum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hieracium sp. et Sonchus arvensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lapsana communis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Linaria spuria</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lycbhis vespertina</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Medicago lupulina</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Mentha arvensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Plantago lanceolata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Plantago media et major</i>	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Polygonum convolvulus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ranunculus arvensis</i>	—	—	—	5	—	9	7	7	4	—	—	—	—	—	—	—	—	—	—
<i>Ranunculus repens</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
<i>Rubus caesius</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Scandix pecten Veneris</i>	—	—	—	1	—	—	1	1	1	—	—	—	—	—	—	—	—	—	—
<i>Senecio vulgaris</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Veronica agrestis</i>	—	—	—	11C	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Veronica Buxbaumii</i>	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Viola tricolor</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Drilled with clover

Crop cut

PLOT VI. *Wheat.*

	<i>Agropyrum repens</i>	<i>Brassica sinapis</i>	<i>Cerastium vulgatum</i>	<i>Cnicus arvensis</i>	<i>Convolvulus arvensis</i>	<i>Euphorbia exigua</i>	<i>Galium aparine</i>	<i>Hieracium</i> sp. et <i>Sonchus</i> <i>arvensis</i>	<i>Lychnis vespertina</i>	<i>Medicago lupulina</i>	<i>Polygonum aviculare</i>	<i>Scabiosa succisa</i>	<i>Senecio vulgaris</i>	<i>Tussilago Farfara</i>	<i>Veronica Buxbaumii</i>	<i>Viola tricolor</i>
Jan. 30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Feb. 28	—	9C	—	—	—	—	—	—	—	—	—	—	—	—	2C	—
Mar. 30	—	13C	—	—	—	—	—	—	—	—	—	—	—	2	7	—
April 16	—	13	—	3	—	—	—	—	—	—	—	—	—	5	4	—
„ 30	—	21	—	5	—	—	—	—	—	—	—	—	—	7	4	—
May 15	—	13	—	3	—	—	—	—	—	—	—	—	—	7	—	—
„ 29	6	5	—	3	5	4	—	1	—	—	—	—	—	7	—	—
June 15	—	15	—	2	3	1	—	1	1	—	—	—	—	7	1	—
„ 30	5	11	—	2	6	1	—	—	—	—	—	—	—	7	2	—
July 15	5	3	—	1	8	1	—	—	—	2	—	—	—	9	2	2
„ 30	5	—	—	2	5	3	1	—	—	—	—	1	—	12	—	2
Aug. 14	16	—	—	5	5	6	—	1	—	2	—	—	—	13	1	2
„ 15-29	Crop cut															
„ 30	16	—	—	6	4	2	—	—	—	—	—	—	—	12	1	1
Sept. 1-16	Sheep fed 1 day															
„ 16	16	—	—	2	1	1	—	—	—	1	3	—	1	10	2	1
„ 30	16	—	—	7	4	2	—	—	—	—	—	—	1	6	1	1
Oct. 31	16	—	1	2	—	—	—	—	—	2	—	—	1	3	5	4
Nov. 30	16	—	—	—	—	—	—	—	—	—	—	—	1	—	17	4
Dec. 30	32	—	—	—	—	—	—	—	—	—	—	—	1	—	17	5

The tables show very well the way certain species suddenly appear in large numbers on a field, especially after disturbance of the soil by one or other of the ordinary agricultural operations. The species may establish itself throughout the season and show a series of individuals all growing to maturity or it may suddenly die away and disappear from the field altogether. The causes of this are difficult to understand. There would appear to be no special reason why the young plants of one particular species should be attacked by animals or disease more than any other or why, in the case of rapidly maturing annuals, a second crop should not be produced. It will be noted that the cycles of variation of numbers of the quickly growing annuals on the plots are a fair indication of their life period; each wave of numbers representing a generation.

The success of ordinary farm tillage in keeping down annuals is also well shown and the complete disappearance of the dead plants was one of the surprises of the investigation. Stubble fields show for a considerable time the stumps of the cereal crop, and the appearance of uncut grasslands in the

autumn when the dead remains or "aftermath" of the grasses cover the ground is well known. The dead leaves and stalks of perennial weeds remain attached to the roots long after dying away and the species can be readily identified, but the annuals seem to disappear entirely in a very short time. The two main factors are probably (1) worms, and (2) fungi of the *Botrytis* type which cause exceedingly rapid disintegration of dead plant tissues. The authors hope to carry on these records and at some future time to investigate especially the question of the decay and disappearance of the annual plants of arable land.

Perennials were only counted when active growth was taking place or when the plant was obviously showing as a "weed." The sudden disappearance and reappearance of isolated individuals therefore means that some accidental cause had deprived the plant of leaves and stem before the count was made. A second growth would lead to its inclusion later on and apparently show it as a fresh individual.

The series show very well how easily the single count may lead to considerable error when determining the relative dominance or rarity of plants forming the arable land flora and would seem to indicate the reason why contradictory results are sometimes obtained when a casual visit is made to any area and only a single examination made of the special fields selected.

THE BRYOPHYTES AND LICHENS OF CALCAREOUS SOIL¹

By W. WATSON.

It is well known that some flowering plants are characteristic of calcareous soils whilst others are absent or extremely rare. The cryptogamic vegetation is similarly affected by the presence or absence of calcium carbonate. In the Oolitic districts of East Somerset, where the foxglove is absent, calcifuge mosses such as *Polytricha*, *Campylopi* and *Sphagna* do not occur, and the same phenomenon is shown in other calcareous tracts. A striking example of the effect of lime on vegetation is shown at Bugsworth in Derbyshire. The soil is siliceous, but is well limed owing to the transport of lime, by means of a narrow gauge railway, from Doveholes. In the vicinity of the railway, and especially where unloading for transport to the main line occurs, calciphilous bryophytes and other plants are abundant.

Many bryophytes and lichens are absent or very rare in calcareous districts. Some of the most pronounced and commonest calcifuge species are:

<i>Sphagnum</i> spp.	<i>Hypnum</i> fluitans	<i>Parmelia</i> saxatilis
<i>Polytrichum</i> spp.	<i>H. exannulatum</i>	<i>P. physodes</i>
<i>Dichodontium</i> pellucidum	<i>H. revolvens</i>	<i>P. omphalodes</i>
<i>Dicranella</i> heteromalla	<i>Aneura</i> multifida	<i>P. sulcata</i>
<i>D. cerviculata</i>	<i>Pellia</i> epiphylla	<i>Lecanora</i> parella
<i>D. squarrosa</i>	<i>Alicularia</i> scalaris	<i>L. polytropa</i>
<i>Campylopus</i> spp.	<i>Gymnocolea</i> inflata	<i>Pertusaria</i> dealbata
<i>Leucobryum</i> glaucum	<i>Leptosecyphus</i> anomalus	<i>Stereocaulon</i> spp.
<i>Racomitrium</i> spp.	<i>Cephaloziella</i> byssacea	<i>Lecidea</i> contigua
<i>Hedwigia</i> ciliata	<i>Lepidozia</i> setacea	<i>L. crustulata</i>
<i>Orthotrichum</i> rupestre	<i>L. reptans</i>	<i>L. granulosa</i>
<i>Aulacomnium</i> palustre	<i>Scapania</i> undulata	<i>L. uliginosa</i>
<i>Pterygophyllum</i> lucens	<i>S. dentata</i>	<i>Rhizocarpon</i> geographicum
<i>Hyocomium</i> flagellare	<i>Sphaerophorus</i> spp.	<i>R. confervoides</i>

A few of these may be found on limestone heath where the top layer of soil is free from lime, or they may extend from a siliceous to a neighbouring calcareous substratum, but a full examination of such exceptions does not contradict but rather emphasise their calcifuge character. On "mixed" walls made up of both siliceous and calcareous stones, near the boundary between siliceous and calcareous outcrops, or when flint or an eruptive rock occurs in limestone, such exceptions may occur, but it is more usual to find that the calciphilous plant has invaded the siliceous substratum.

¹ Part of a thesis accepted for the degree of D.Sc. at the University of London.

There are many "indifferent" plants of all groups which are abundant both on calcareous and siliceous substrata. The following bryophytes and lichens may fairly be considered "indifferent":

Mosses :

<i>Grimmia apocarpa</i>	<i>Catharinea undulata</i>	<i>Plagiothecium silvaticum</i>
<i>Tortula muralis</i>	<i>Mnium undulatum</i>	<i>P. denticulatum</i>
<i>Fissidens bryoides</i>	<i>Neckera complanata</i>	<i>Amblystegium serpens</i>
<i>Bryum capillare</i>	<i>Porotrichum alopecurum</i>	<i>Hypnum riparium</i>
<i>B. caespiticiu</i>	<i>Brachythecium rutabulum</i>	<i>H. cupressiforme</i>
<i>B. pallens</i>	<i>Eurhynchium praelongum</i>	<i>Hylocomium triquetrum</i>
<i>Thuidium tamariscinum</i>	<i>E. striatum</i>	<i>H. squarrosum</i>
<i>Dicranum scoparium</i>		

Liverworts :

<i>Plagiochila asplenioides</i>	<i>Aplozia riparia</i>	<i>Scapania nemorosa</i>
<i>Lophocolea cuspidata</i>	<i>Calypogeia fissa</i>	<i>Lejeunea cavifolia</i>
<i>Cephalozia bicuspidata</i>		

Lichens :

<i>Peltigera canina</i>	<i>Urecolaria scruposa</i>	<i>Buellia canescens</i>
<i>P. polydactyla</i>	<i>Cladonia pyxidata</i>	<i>Verrucaria muralis</i>
<i>Lecanora campestris</i>	<i>C. furcata</i>	<i>Dermatocarpon miniatum</i>

Other common bryophytes and lichens which are almost "indifferent" but show a slight preference for limestone districts are:

<i>Grimmia pulvinata</i>	<i>Anomodon viticulosus</i>	<i>Leptogium lacerum</i>
<i>G. apocarpa</i>	<i>Camptothecium sericeum</i>	<i>L. pulvinatum</i>
<i>Tortula ruralis</i>	<i>Eurhynchium rusciforme</i>	<i>L. scotinum</i>
<i>Bryum inclinatum</i>	<i>E. swartzii</i>	<i>L. tenuissimum</i>
<i>B. pendulum</i>	<i>Aneura pinguis</i>	<i>Dermatocarpon lachneum</i>
<i>Fontinalis antipyretica</i>	<i>Madotheca platyphylla</i>	<i>D. hepaticum</i>

There are many plants which are never found except on calcareous rocks and soils and many others which show a decided preference for such habitats. These calcicole species are indicated in the following lists by an asterisk.

Many plants which are usually given as showing a preference for calcareous soil are probably calcicole species in a stricter sense than is generally understood. In many instances departures from their calcicolous character have been shown by a detailed study to be more apparent than real, and probably other ecological unconformities would yield similar results after fuller investigations.

In the Millstone Grit districts of the Pennines *Barbula tophacea* and *Encalypta streptocarpa* grow together on siliceous walls but only on damp mortared walls. When dry walling (i.e. building walls without the use of mortar) is practised in the same district one searches such walls in vain for either of these mosses.

Tortula ambigua and *T. aloides* usually occur in calciferous soil but are often present on Triassic sandstone of mortared walls in Somerset.

When limestone is sufficiently near to siliceous rock, the latter is often invaded by calcicolous species, a sufficient quantity of lime being imported by wind or water to enable them to exist, though often in a depauperate condition. On the boundaries between limestone and sandstone outcrops, as on Rushup Edge in Derbyshire, calcicolous plants such as *Encalypta streptocarpa* and *Collema multifidum* (= *C. melaenum*) occasionally occur on the sandstone. On flint and chert *Verrucaria integra*, *V. glaucina*, *V. nigrescens*, *Pannularia nigra* and other lichens occasionally spread from the surrounding calcareous rock. Where an eruptive rock occurs in limestone invasions from calcareous to siliceous rock or *vice versa* may sometimes occur, but mistakes in recording the habitat are more likely. Such an intermixture of rock occurs near the Sychnant brook on the Minera mountain of Denbighshire, and the notes made during my first examination of its bryophytic flora required careful revision later on when it was realised how deceitfully the rocks were intermixed. Similar care has to be taken in some parts of Derbyshire where toadstone occurs.

Weisia tenuis probably has a much more decided preference for lime-containing rocks than is generally thought. On a sandstone at Tinkerborough near Stafford I found it growing abundantly. On the same sandstone, *Barbula tophacea*, *Pellia fabbronia*, *Amblystegium filicinum*, *A. serpens*, *Bryum capillare*, *Brachythecium rutabulum*, *Webera albicans*, *Tortula muralis* and *Barbula fallax* were present. The first three bryophytes are calciphilous and on testing the sandstone with weak acid a decided effervescence indicated the presence of carbonate of lime. Many sandstones on which this moss grows are distinctly calciferous and an ecologist requires some weak acid in his field equipment. Another calcicolous plant which is not uncommon in such a habitat is the crustaceous lichen, *Pannularia nigra*.

The occurrence of *Lophozia turbinata* and *Barbula cylindrica* by road-side ditches has, in several instances, been traced to the use of limestone for road-mending. In some other cases of deviation by these two plants from their normal calcareous habitat, the deviation could not be shown to be an apparent one.

The aberrant occurrence of some calcicole bryophytes on siliceous grassland may sometimes be traced to the frequent liming of the land.

Many calcicole plants occur on sand-dunes, but since comminuted shells are present there is sufficient lime for their requirements.

The lichens of calcareous walls are often very noticeable and characteristic and this is especially true for crustaceous lichens. On "dry" walls built up with both calcareous and siliceous stones some species may be erratic but usually the components of the wall are well differentiated by their drapings of lichens. Near Mam Tor in Derbyshire such a wall occurs. The siliceous stones are well marked by the presence of *Parmelia saxatilis*, *P. sulcata*, *P. physodes*, *Lecanora polytropa* and *Lecidea contigua*, whilst the limestone is clothed with

Placodium aurantium var. *plicatum* (= *Lecanora sympagea* of Crombie's Monograph), *Verrucaria calciseda*, *V. nigrescens*, *Thelidium immersum*, *Collema multifidum*, *Xanthoria parietina*, *Physcia caesia*, *Lecanora galactina* and *Aspicilia calcarea*.

The factors influencing the distribution of the higher plants are both chemical and physical and there is some doubt as to the relative importance of these factors. In regard to many bryophytes and lichens there seems little room to doubt that the chemical factor is much more important. Lichens with deeply-immersed reproductive bodies always occur on some form of limestone since siliceous rocks are less able to be attacked by an acid excretion. Many calcicole bryophytes and lichens are indifferent to the physical character of the substratum, they will grow on almost any rock or soil if calcium carbonate is present. *Hypnum molluscum* is a striking example of this indifference. It occurs most abundantly on damp and somewhat shady limestone soil, but also occurs on sandy, marly, or clayey soil, on calciferous sandstone and sand-dunes, or on igneous or metamorphic rocks and their products of decomposition. It occurs on Precambrian, Cambrian, Silurian, Devonian, Carboniferous, Permian, White Lias, Jurassic and Cretaceous lime-containing rocks or soil. In all cases which I have fully investigated the substratum has had lime contents. The only habitat in which I have found this moss and have been unable to prove the presence of lime is by some mountain streams, and even then its association with other bryophytes which are usually calciphilous renders the presence of lime probable. *Ditrichum flexicaule* and *Trichostomum tortuosum* have a similar varied habitat, and detailed examination of the substratum similarly reveals the presence of lime. In any case too much importance must not be attached to the exceptional occurrence of calciphilous bryophytes on a lime-free soil or rock.

The Chalk:

The Chalk has not been sufficiently studied to give a detailed account of its cryptogamic flora. General examination indicates that the difference between the distribution of the bryophytes and lichens on the older limestones and on the Chalk are slight, and that ecological classification would follow similar lines. The shade due to the close leafy canopy in the beechwood causes considerable differences between its ground flora and that of the ashwood. In the deepest shade the only plants present may be such saprophytic fungi as *Marasmius peronatus*, *Collybia dryophila*, *Boletus felleus*, *Cantharellus cibarius* and *Mycena pura*. In more open places and especially when rocks are abundant, the bryophytes and lichens are similar, particularly if places with similar light intensities are compared. A few calcicole species are seldom found except on chalk, the only frequent one being *Seligeria calcarea*. *S. paucifolia*, *Thuidium hystricosum*, *Weisia sterilis*, *Dicranum bonjeani* var. *calcareum*, *Cephaloziella baumgartneri*, *Lecidea obsoleta*, *Thelidium microcarpum*, *T. sparsulum* and *Polyblastia schraderi* are rare and mostly local plants.

The Older Limestones.

The ashwood association is characteristic of the Carboniferous limestone, and this has been particularly examined on the Mendip and in less detail in Derbyshire, Flintshire, Denbighshire, Wye Valley (with a Beechwood association) and Wharfedale. Limestones of other formations which have been studied include the Devonian limestone of S. Devon and small patches in W. Somerset, the Woolhope limestone, the Dolomitic Conglomerate flanking the Mendip, the Magnesian limestone of Yorkshire, the White Lias near Taunton, and the Jurassic limestones of E. Somerset.

The ground flora of the actual wood contains such bryophytes as

<i>Hypnum molluscum</i> * sd	<i>Porotrichum alopecurum</i> a	<i>F. incurvus</i> o
<i>H. cupressiforme</i> a	<i>Mnium undulatum</i> a	<i>F. decipiens</i> * f
var. <i>clatum</i> * o	<i>M. cuspidatum</i> a	<i>Ditrichum flexicaule</i> * f
<i>H. chrysophyllum</i> * o	<i>M. rostratum</i> * a	<i>Dicranum scoparium</i> a
<i>H. hispidulum</i> var. <i>sommerfeltii</i> * o	<i>M. affine</i> a	<i>D. majus</i> o
<i>Hylocomium triquetrum</i> a	<i>M. stellare</i> o	<i>Catharina undulata</i> a
<i>H. squarrosum</i> o	<i>M. hornum</i> a	<i>Metzgeria furcata</i> (usually on trees) a
<i>Amblystegium serpens</i> o	<i>Bryum capillare</i> a	<i>Lophozia turbinata</i> * f
<i>Eurhynchium striatum</i> a	<i>Encalypta streptocarpa</i> * f	<i>Plagiochila asplenioides</i> and var. <i>major</i> a
<i>E. tenellum</i> * f	<i>Barbula fallax</i> a	<i>Chiloscyphus pallescens</i> o
<i>E. praelongum</i> a	<i>B. cylindrica</i> * a	<i>Lophocolea cuspidata</i> a
<i>E. crassinervium</i> f	<i>B. unguiculata</i> o	<i>L. bidentata</i> o
<i>E. confertum</i> o	<i>B. rubella</i> o	<i>Cephalozia bicuspidata</i> a
<i>Plagiothecium denticulatum</i> a	<i>Trichostomum crispulum</i> * o	<i>Calypogeia fissa</i> o
<i>P. silvaticum</i> a	<i>T. tortuosum</i> * o	<i>Scapania aspera</i> * a
<i>Brachythecium rutabulum</i> a	<i>Tortula subulata</i> o	<i>S. nemorosa</i> o
<i>B. velutinum</i> o	<i>T. ambigua</i> * f	<i>Madotheca platyphylla</i> f
<i>Thuidium tamariscinum</i> a	<i>Weisia crista</i> * o	<i>Marchesinia mackaii</i> * f
<i>Neckera complanata</i> a	<i>Fissidens viridulus</i> o	<i>Lejeunea cavifolia</i> o
<i>Camptothecium sericeum</i> o	<i>F. taxifolius</i> o	
<i>Anomodon viticulosus</i> a	<i>F. bryoides</i> o	

Lichens are not abundant in the well-shaded portions of the wood but the following occur on the shaded rocks and ground: *Collema auriculatum* * o, *C. granosum* * o, *C. pulposum* f, *C. ceranoides* * o, *Leptogium pusillum* o, *L. lacerum* o, *L. scotinum* o, *Stictina fuliginosa* o, *Peltigera canina* f, *P. polydactyla* o, *P. horizontalis* o.

The arboreal cryptogams are not included in the above list, nor in the following lists. Their abundance and diversity are influenced chiefly by the humidity and purity of the atmosphere.

In the wet or moist places of the wood the calciphilous plants *Amblystegium filicinum*, *Hypnum commutatum*, *Eurhynchium teesdalei*, *Orthotrichum rivulare*, *Barbula cylindrica*, *Weisia rupestris*, *W. verticillata*, *Pellia fabbroniana*, *Preissia quadrata*, *Lophozia turbinata*, together with the "indifferent" plants *Hypnum riparium*, *H. cuspidatum*, *Brachythecium rivulare*, *B. plumosum*, *Eurhynchium*

* = calcicole.

rusciforme, *Porotrichum alopecurum*, *Mnium punctatum*, *Fontinalis anti-pyretica*, *Aplozia riparia*, *Chiloscyphus polyanthus*, *Conocephalum conicum* and *Cephalozia bicuspidata*, are usually frequent.

Ash Scrub. In drier parts of the ash wood, in what is better described as ash scrub, and on more or less shaded limestone cliffs and screes, the bryophytes and lichens are similar and consist of such plants as:

Hypnum molluscum * a	Dicranum scoparium a	C. plicatile * o
H. cupressiforme a	Seligeria pusilla * lf	Peltigera polydactyla f
Eurhynchium circinatum * la	Fissidens decipiens * f	P. rufescens f
E. striatulum * o	Weisia tenuis * o	P. canina f
E. swartzii f	W. calcarea * o	Solorina saccata * f
Camptothecium sericeum a	W. crispata * o	Squamaria crassa * f
C. lutescens * o	W. tortilis * o	Placodium aurantium and
Neckera crispa * a	W. microstoma o	var. plicatum * f
Mnium rostratum * f	Zygodon stirtoni o	P. cirrochroum * o
M. stellare o	Z. viridissimus o	P. granulosum * r
M. undulatum f	Targionia hypophylla * o	Callopisma ochraceum * o
Thuidium philiberti * f	Reboulia hemisphaerica * o	C. tetrastichum * o
T. tamariscinum f	Aneura pinguis and var. den-	C. irrubatum * f
Anomodon viticulosus a	ticulata o	C. calvum * f
A. longifolium * l	Metzgeria pubescens * lf	C. erythrellum o
Bryum provinciale * lf	M. furcata (usually on trees) o	Leproplaca xantholyta * lf
B. capillare a	Lophozia turbinata * o	Diphrotora candicans * f
Pleurochaete squarrosa o	L. badensis * o	Candelaria vitellina o
Trichostomum tortuosum * a	Pedinophyllum interruptum	Pyrenodesmia variabilis * o
T. crispulum * a	* r	P. chalybaea * o
T. nitidum * f	Plagiochila asplenioides a	Lecanora galactina * a
T. mutabile * f	var. humilis f	L. campestris a
Orthotrichum anomalum	Lophocolea cuspidata a	Rinodina bischoffi var. im-
var. saxatile * f	Scapania aspera * a	mersa * r
O. cupulatum * o	Madotheca platyphylla a	Aspicilia calcarea * a
O. diaphanum o	Cololejeunea calcarea * o	A. prevostii * lf
Funaria calcarea * f	C. rossettiana * r	Urceolaria gypsacca * lf
Encalypta vulgaris * a	Frullania dilatata and F. ta-	U. scruposa o
E. streptocarpa * f	marisci (usually on trees) o	U. bryophila o
Barbula fallax a	Cladonia pyxidata and var.	Gyalecta exanthematica * f
B. rigidula * o	pocillum o	G. cupularis * f
B. sinuosa * o	Pannularia nigra * o	Lecidea lurida * a
B. revoluta * a	Synalissa symphorea * r	L. decipiens * o
B. rubella f	Collema auriculatum * f	L. testacea * l
Tortula intermedia * a	C. granosum * f	L. immersa * a
T. ruralis f	C. furvum * f	L. metzleri * l
T. muralis a	C. tenax and C. crispum f	Biatorina coeruleonigricans
T. aloides * f	C. pulposum f	* a
T. ambigua * f	C. granuliferum * a	B. candida * lf
Grimmia apocarpa a	C. multifidum * a	B. lenticularis f
G. pulvinata a	C. multipartitum * r	Buellia canescens f
G. orbicularis * o	Collemodium schraderi * f	Bilimbia aromatica * a
Ditrichum flexicaule * f	C. turgidum f	B. sabuletorum f

Dermatocarpon miniatum, and var. complicatum o	Verrucaria nigrescens * a	Thelidium immersum * f
D. hepaticum o	V. coerulea * o	Staurothelo ebborensis * l
D. lachneum o	V. rupestris * o	Acrocordia epipolaea * f
	V. calciseda * a	

Exposed Limestone Rocks.

On exposed rocks and on calcareous walls the bryophytes and lichens are very characteristic and prominent constituents of the vegetation. Most of the species of the following list are found on limestone walls.

Grimmia apocarpa a	O. cupulatum * o	P. virella f
G. pulvinata a	Bryum pendulum f	Squamaria saxicola a
G. orbicularis * o	B. capillare a	Placodium murorum, form
Weisia viridula o	B. inclinatum a	pulvinatum * a
Trichostomum crispulum * o	B. murale * f	P. aurantium * f
T. nitidum * o	B. caespitium f	var. plicatum * a
Encalypta vulgaris * f	Camptothecium sericeum sd	Callophisma citrinum * a
E. streptocarpa * f	Hypnum hispidulum, var.	C. irrubatum * f
Tortula muralis a	sommerfeltii * o	C. calvum * f
var. rupestris * f	Madotheca platyphylla o	Diphtratora candicans * f
T. aloides * f	Plagiochila asplenioides, vars.	Candelaria vitellina f
T. ambigua * o -	minor and humilis r	Lecanora galactina * a
T. ruralis a	Pannularia nigra * a	L. crenulata * f
T. intermedia * f	C. furvum * o	L. campestris a
Barbula rigidula * o	C. pulposum f	Lecania erysibe f
B. fallax a	C. cheileum * a	Aspicilia calcarea * a
B. hornschiuchiana f	C. granuliferum * f	Acarospora pruinosa * a
B. sinuosa * o	C. multifidum * f	Lecidea immersa * f
B. revoluta * a	C. polycarpon * o	L. ochracea * o
B. convoluta o	Collemodium turgidum f	L. fusciorubens o
B. lurida * o	Leptogium pulvinatum a	L. sympathetica f
Orthotrichum anomalum,	Xanthoria parietina a	Bilimbia aromatica * f
var. saxatile * a	Physcia tenella a	B. sabuletorum f
O. diaphanum f	P. caesia a	Buellia canescens f

Limestone Grassland Association.

In the actual grassland few bryophytes or lichens occur but they become more frequent in moist or wet parts, and when the surface is rocky they become abundant. On "calcareous heath" they are often very abundant, but consist of plants which are indifferent to lime conditions or may even be calcifuge. Sphagna, Polytricha, Campylopi, Dicrana, Rhacomitria, Dicranellae, Plagiothecia, Diplophylla, Lophozia, Lepidozia and other plants which may be abundant on such heaths are rarely found in calcareous districts. If present, their rhizoids do not penetrate to the calcareous substratum, and the plants really live on non-calcareous soil.

The commonest mosses on dry calcareous pasture (e.g. Brean Down (Carboniferous limestone), slopes of Castleton, are (*after the name indicates that the species shows a preference for a calcareous substratum):—*Fissidens decipiens* * (form of grassy ground), *Dicranum scoparium*, *Barbula fallax*,

Weisia crispata *, *Ceratodon purpureus*, *Trichostomum crispulum* *, *Bryum capillare*, *Camptothecium lutescens* *, *Brachythecium rutabulum*, *B. glareosum* *, *Eurhynchium swartzii*, *E. pumilum*, *Hypnum molluscum* *, *H. cupressiforme*, *Hylocomium squarrosum*. Where the ground becomes more stony *Ditrichum flexicaule* *, *Funaria calcarea* *, *Encalypta vulgaris* *, *E. streptocarpa* *, *Tortula ambigua* *, *T. aloides* *, *Bryum caespitium*, *Neckera crispa* *, *Anomodon viticulosus*, *Camptothecium sericeum* *, *Hypnum chrysophyllum* *, *H. hispidulum* var. *sommerfeltii* *, occur, but all these are more frequent on the actual rock or its soil-cap.

Other plants which are frequent in damper places are *Barbula cylindrica* *, *Webera albicans*, *Bryum pallens*, *Thuidium recognitum* *, *T. philiberti* *, *Hypnum cuspidatum*.

Some calcicole plants of limestone grassland such as *Weisia tortilis* and *Cylindrothecium concinnum* are less frequent or local in distribution.

Polytricha, Rhacomitria, Dicrana, Dicranellae, Mnia, Weberae and Plagiothecia are commoner on siliceous grassland, but *Dicranum scoparium*, *Mnium stellare*, *M. hornum*, *Plagiothecium denticulatum* and *P. undulatum* have been met with in abundance on some Carboniferous limestone pasture (Castleton). The hepatics of grassland are not abundant. *Lophocolea cuspidata*, *L. bidentata* and *Plagiochila asplenioides* are the liverworts most frequently found, and show little preference for calcareous or siliceous soil.

Lichens are occasionally found, usually on bare places but sometimes amongst short grass, *Cladonia sylvatica* and *C. furcata* often being plentiful on wind-swept summits. The following lichens are occasional members of this association: *Collema pulposum*, *C. crispum*, *Collemodium turgidum*, *Leptogium tenuissimum*, *L. lacerum*, *Peltigera canina*, *P. rufescens*, *P. polydactyla*, *Cladonia pungens*, *C. furcata*, *C. sylvatica*. None of these, with the probable exception of the Collemaceous plants, can be considered as calcicolous plants.

Association of Limestone Pavements.

A limestone pavement near Bwlch Gwyn in Denbighshire is an excellent example, and has been particularly studied in compiling the following list of bryophytes and lichens.

Seligeria calcarea * f
S. pusilla f
Trichostomum crispulum * a
 var. *nigroviride* * f
Ditrichum flexicaule * a
 var. *densum* * f
Dicranoweisia cirrata o
Grimmia apocarpa a (in dry places the apical portion of the leaf has little chlorophyll)
G. pulvinata a

Fissidens decipiens * f
Tortula intermedia * a
T. muralis a
 var. *rupestris* f
Barbula lurida * a
B. rigidula * a
B. cylindrica * f
B. fallax f
B. tophacea * o
B. hornschiuchiana o
B. revoluta * o

- Trichostomum tortuosum* * a
T. mutabile v. *cophocarpum* * o
Weisia calcarea * o
W. verticillata * o (moist)
W. tortilis * o
W. tenuis * o
Zygodon mougeotii o
Bartramia pomiformis o
Encalypta streptocarpa * a
E. vulgaris * o
Funaria calcarea * o
Orthotrichum anomalum v. *saxatile* * a
Bryum capillare a
 var. *ferchellii* * f
 var. *rosulatum* o
Mnium stellare o
M. rostratum * a
Orthothecium intricatum o
Neckera complanata o
N. crispa * a
 var. *falcata* * a (drier places)
Camptothecium lutescens * o
C. sericeum f
Brachythecium velutinum o
Amblystegium serpens o
A. filicinum * (moist places) o
Hypnum hispidulum var. *sommerfeltii* * o
H. cupressiforme f
 var. *tectorum* f
H. molluscum * a
Targionia hypophylla * o
Conocephalum conicum (moist places) o
Reboulia hemisphaerica * o
Aneura pinguis o
Riccia lescuireana o (in hollows where
 water stands)
Pellia fabbronia * (moist places) o
Metzgeria pubescens * l
Lophozia badensis * o
L. turbinata o
L. ventricosa r
Plagiochila asplenioides o
Pedinophyllum interruptum * l
Diplophyllum albicans r
Scapania aspera * f
Madotheca platyphylla o
Frullania tamarisci f
Collema granuliferum * f
C. flaccidum * o
C. multifidum * f
C. auriculatum * o
C. furvum * o
C. crispum o
C. pulposum f
Leptogium lacerum f
L. pulvinatum f
Synalissa symphorea * r
S. intricata r
Solorina saccata * f
Pannularia nigra * a
Peltigera canina f
Xanthoria parietina a
Squamaria crassa * f
Placodium aurantium * f
 var. *plicatum* * f
P. murorum, form *pulvinatum* * o
Diphrotora candicans * f
Lecanora campestris * a
L. galactina * f
Aspicilia calcarea * a
A. prevostii * r
Lecidea immersa * a
Biatorina coerulca nigricans * a
Bilimbia aromatica * o
B. sabuletorum o
Acarospora pruinosa * f
Verrucaria integra * f
V. rupestris * f
V. nigrescens * f
V. calciseda * f
Thelidium immersum * o
Trentepohlia aurea f

Many slight variations in the actual habitats of these plants are shown, some occurring on the rock faces, others on the crumbling sides of the fissures, others only in the moister places. Such mosses as *Tortula intermedia*, *Encalypta vulgaris*, *Camptothecium sericeum*, occur on the exposed faces of the rock, whilst *Fissidens decipiens*, *Barbula cylindrica*, etc. prefer less exposed and damper situations. The only hepatic which occurs at all commonly on the exposed surfaces is *Frullania*, but the lichens are more frequent there than in any

other situation. Where light-intensity becomes small lichens are absent and few bryophytes occur. In a general way the bryophytes and lichens of limestone pavements are similar to those found on calcareous rocks and walls, and a list of bryophytes and lichens from limestone cliffs would largely consist of the same species as have been given above for the limestone pavement.

A few lichens are able to excrete some acid juice beneath the developing reproductive bodies, so that the apothecia lie in small pits. These pits are well developed in *Thelidium immersum*, *T. incavatum*, *Lecidea immersa*, *Verrucaria calciseda*, *V. integra*, *V. rupestris* and *Aspicilia prevostii*. In these lichens, the acid excretion pits the rock so deeply that only the tops of the apothecia can be seen. A smaller amount of pitting also occurs in *Lecidea metzleri*, *L. contigua* form *calcareo*, *Rhizocarpon calcareum*, *Arthopyrenia foveolata* and *Rinodina bischoffii* var. *immersa*.

AN ECOLOGICAL SURVEY OF THE HAWAIIAN PTERIDOPHYTES

BY VAUGHAN MACCAUGHEY,

Professor of Botany, College of Hawaii, Honolulu.

The pteridophytes of the Hawaiian Archipelago have been collected and studied taxonomically by a considerable number of investigators, the most important work being that of Hillebrand (7) and Robinson (12). In this taxonomic work little or no emphasis has been placed upon the ecological relationships of these plants. It is the purpose of the present paper particularly to consider the latter topic, with special reference to distribution and endemism.

In the Hawaiian Islands there are forty-four genera and 190 recorded species of pteridophytes. Of these two genera, *Diellia* and *Sadleria*, are endemic, and 195 species are endemic. There is no other region in the world with so high a percentage of endemism as Hawaii. Thirty-three species in the islands are practically cosmopolitan, being widely distributed throughout the tropics and sub-tropics; twenty species have the South Pacific as their chief station, and six species have the West Coast of America as their distribution centre.

Guppy (6) points out that in Hawaii, Fiji and Tahiti the "pteridophytes have been largely supplied from the warmer regions of the Old World. But whilst in the South Pacific the migration has been mainly from Fiji eastward to Tahiti, it is probable that Hawaii in the North Pacific has been in part independently stocked. Whilst there has been more or less free immigration into Fiji and Tahiti there has been comparative isolation in Hawaii. Though the areas of the Fijian and Hawaiian archipelagos are about the same, Fiji possesses at least half as many species again as Hawaii, but Hawaii owns three or four times the number of peculiar species.

"Whilst a large proportion of the pteridophytes are common to all three groups, Hawaii possesses a number of mountain species, widely distributed in temperate regions and on the higher levels of mountainous areas in the tropics, that are not found either in Fiji or Tahiti. Their absence from these two groups is due to the insufficient elevation of the islands and to the non-existence there of extensive areas of any altitude."

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The representation of genera in the Hawaiian flora, on the basis of number of species, is as follows:

1. GENERA WITH ENDEMIC SPECIES.

Genus	Total no. species in islands	No. of endemic species
Ophioglossum	4	1
Botrychium	1	1
Marattia	1	1
Trichomanes	5	1
Hymenophyllum	4	3
Cibotium	3	3
Elaphoglossum	9	6
Pteris	5	2
Histiopteris	1	1
Doryopteris	2	2
Hypolepis	2	1
Schizostege	1	1
Diellia	8	8
Odontoloma	1	1
Filix	1	1
Dryopteris	21	15
Polypodium	15	14
Polystichum	3	2
Cyrtomium	2	1
Asplenium	38	27
Athyrium	9	9
Diplazium	3	2
Sadleria	7	7
Doodya	1	1
Dicranopteris	2	2
Schizaea	1	1
Marsilea	2	2
Lycopodium	10	5
Selaginella	4	2

2. GENERA WITH NO ENDEMIC SPECIES.

Genus	Total no. species in islands
Pteridium	1
Pellaea	1
Adiantum	2
Nephrolepis	2
Odontosoria	2
Microlepia	2
Vittaria	1
Ceropteris	2
Coniogramme	1
Phymatodes	2
Phlebodium	1
Tectaria	1
Neottopteris	1
Azolla	1
Psilotum	2

It will be noted that the most important genera are *Asplenium*, *Dryopteris*, *Polypodium*, *Lycopodium*, *Athyrium* and *Diellia*, *Elaphoglossum*. The genera with no endemic species are relatively recent additions to the flora, and are waifs and strays that have arrived from various quarters.

The distribution of the ferns upon the various islands of the group is very significant, and furnishes the most striking corroboration of the generally-accepted idea (10) that the westward islands are older, and longer isolated, than the eastern. The island of Kauái, the Waianae range on Oahu, East Molokái, West Maui, and the Kohala Mountains, Hawaíi, are the older portions of the archipelago, and it is exactly in these regions that the fern-flora is most abundant and diversified. It should be noted in passing that extensive areas on all the islands, once forested and fern-habited, are now barren and deforested. Kauái contains the largest number of endemic species and varieties, and Oahu stands second. These two islands possess more peculiar species than all the other islands combined. In the following table the numbers indicate the number of species found in the region indicated, and recorded from no other part of the archipelago:

Kauái only	19	Oahu to Hawái	2
Kauái and Oahu	2	Molokái only	1
Kauái to Maui	10	Maui only	5
Kauái and Maui	4	Maui and Hawái	5
Oahu only	11	Lanai only	1
Oahu and Maui	6	Hawái only	1
Oahu to Maui	3	All the larger islands	120

The next table shows the geographic ranges of the species in a representative Hawaian genus, *Diellia*, all members of which are endemic.

	Kauái	Oahu	Molokái	Maui	Hawái
<i>Diellia centrifolia</i>	x	—	—	—	—
<i>pumila</i>	—	x	—	—	—
<i>erecta</i>	x	x	x	x	—
<i>Alexandri</i>	x	—	—	x	—
<i>falcata</i>	—	x	—	x	—
<i>laciniata</i>	x	—	—	—	—
<i>Knudsenii</i>	x	—	—	—	—
<i>Mannii</i>	x	—	—	—	—
	6	3	1	3	0

Hawái, with an area larger than the combined areas of all the other islands, is exceedingly poor in endemic forms.

Among the species with wide geographical ranges, both in the islands and throughout the world, are such as *Ophioglossum vulgatum*, *Trichomanes parvulum*, *Hymenophyllum recurvum*, *Elaphoglossum æmulum*, *Pteris longifolia*, *Pteridium aquilinum*, *Pellaea ternifolia*, *Adiantum capillus-veneris*, *Hypolepis punctata*, *Nephrolepis exaltata*, *Odontosoria chinensis*, *Microlepia strigosa*, *Ceropteris ochracea*, *Dryopteris parasitica*, *Phymatodes elongata*, *Phlebodium aureum*, *Polystichum carvifolium*, *Neottopteris nidus*, *Asplenium unilaterale*, *Dicranopteris linearis*, *Lycopodium serratum*, *Psilotum nudum*. Contrasting sharply with this group are the highly precinctive forms, such as *Trichomanes cyrtotheca*, *Diellia Mannii*, *Diellia centrifolia*, *Dryopteris parvula*, *Polystichum Haleakalaense*, *Asplenium Kauáiense*, *Asplenium Lydgatei*, *Asplenium meiotomum*, *Athyrium Baldwini*, *Lycopodium Haleakalae*.

The ecological zonation of the fern-flora is of particular interest. The great majority of the species, as might readily be expected, inhabit the rain-forests, at elevations of 1000 to 6000 ft. Some species, however, are restricted to the lowlands, or occur chiefly there, at altitudes of 500-1000 ft, or even at sea-level in favourable regions. Examples of this class are *Ophioglossum concinnum*, *Adiantum capillus-veneris*, *Odontosoria chinensis*, *Dryopteris propinqua*, *Asplenium Macraei*, *Sadleria cyatheoides*, *Marsilea villosa* and *Psilotum nudum*.

A second class includes those species that inhabit the lower forest zone, the more open woodlands lying approximately between 1000-2000 ft elevation. Examples of these are *Nephrolepis exaltata*, *Microlepia strigosa*, *Vittaria rigida*, *Ceropteris calomelanos*, *Coniogramme fraxinea*, *Dryopteris nuda*, *Dryopteris cyatheoides*, *Phymatodes elongata*, *Tectaria cicutaria*, *Neottopteris nidus*, *Asplenium lunulatum* and *Athyrium Pioretianum*.

A third class includes those species which are characteristic of the middle forest zone—the rain-forests on the mountain slopes which lie between 1800

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and 3000–5000 ft. The boundaries of this zone are difficult to define sharply, as they vary greatly on the various mountain ranges. On the high mountains of Maui and Hawai'i for example, this zone is much wider and higher than on such islands as Oahu and Kaua'i. *Ophioglossum pendulum*, *Botrychium*, *Marattia*, *Trichomanes*, *Hymenophyllum*, *Cibotium*, *Elaphoglossum*, *Pteris*, *Histiopteris*, *Schizostegia*, *Diellia*, *Odontotoma*, *Vittaria*, *Filix*, *Dryopteris*, *Polypodium*, *Phlebodium*, *Cyrtomium*, *Asplenium*, *Athyrium*, *Diplazium*, *Sadleria*, *Doodia*, *Dicranopteris*, *Psilotum complanatum*, *Lycopodium* and *Selaginella*, are characteristic of this zone.

The fourth zone is the upper forest. On such islands as Oahu, Kaua'i and Molokai, this forest covers the summit ridges and peaks. It is a region of torrential rainfall; the annual precipitation averages over several hundred inches. The summit bogs or swamplands lie at elevations of 3000–6000 ft; some of the summit ridges are at levels of 2000–3000 ft. Many species occur at these elevations which are not found at the lower levels. *Trichomanes radicans*, *Hymenophyllum obtusum*, numerous species of *Elaphoglossum*, *Pteris excelsa*, *Dryopteris decipiens*, *Hypolepis punctata*, *Diella erecta*, numerous species of *Dryopteris* and *Polypodium*, *Polystichum carvifolium*, numerous species of *Asplenium*, *Sadleria Souleytiana*, *Dicranopteris Hawai'iensis*, *Schizaea robusta*, *Lycopodium serratum* and *Selaginella deflexa* are typical pteridophytes of this wet upper zone.

The fifth large ecologic zone is that comprehended by the high summits (7,000–nearly 14,000 ft) of Maui and Hawai'i (10). Hale-a-ka-la, Kea, Loa and Hualalai rise far above the wet zone described in the preceding paragraph. The ferns that occur in this highest zone are xero- or semi-xerophytic in character; several of them occur in many other countries. *Pteridium aquilinum*, *Pellaea ternifolia*, *Dryopteris paleacea*, *Polystichum Haleakalaense*, *Asplenium trichomanes*, *Asplenium adiantum-nigrum*, *Sadleria* spp., *Dicranopteris* spp. are representative of this high summit zone.

There are about sixty species of Hawaiian ferns that are habitually epiphytic, chiefly on trees and tree-ferns, etc.; these are confined almost wholly to the rain-forest zone. There are fifteen or more species that are xero- or semi-xerophytic; these occur at various levels from arid lowlands and coastal situations to the barren summits already mentioned. Eight species attain arborescent stature (11), these are chiefly *Cibotium* and *Sadleria*. About fifteen species are lithophilous, occurring either on detached rocks and boulders in the rain-forests, or on dry ledges and rocky shelves.

The following classification indicates some of the important representatives of the various ecologic groups:

1. DISTINCTIVELY HYGROPHYTIC. *Botrychium*, *Marrattia*, *Trichomanes*, *Hymenophyllum*, *Adiantum*, *Hypolepis*, *Schizostegia*, *Dryopteris*, *Polypodium*, *Schizaea*, *Cibotium*, *Doodia*, *Selaginella*, *Polystichum*, *Asplenium*, *Athyrium*, *Sadleria rigida*, *Psilotum complanatum*.

2. DISTINCTIVELY MESOPHYTIC. *Microlepia*, *Ceropteris*, *Dicranopteris linearis*, *Psilotum nudum*, *Ophioglossum concinnum*, *Elaphoglossum Wawrae*, *Pteris cretica*, *Nephrolepis exaltata*, *Dryopteris rubiformis*, *Neottopteris*, *Asplenium Macraei*, *Asplenium rhipidoneuron*.

3. DISTINCTIVELY XEROPHYTIC. *Pellaea ternifolia*, *Doryopteris decora*, *Diellia falcata*, *Diellia pumila*, *Sadleria cyatheoides*, *Sadleria Hillebrandii*, *Sadleria polystichoides*, *Pteridium aquilinum*, *Asplenium trichomanes*.

4. DISTINCTIVELY HYDROPHYTIC. *Azolla*, *Marsilea*, *Dryopteris propinqua*.

TABLE SHOWING TYPICAL RANGES.

(Figures indicate feet above sea-level.)

500- 2,000	<i>Neottopteris</i>
500- 3,000	<i>Psilotum nudum</i>
500- 5,000	<i>Odontosoria chinensis</i>
500- 6,000	<i>Ophioglossum pendulum</i> , <i>Dryopteris propinqua</i>
700- 1,000	<i>Athyrium Poiratianum</i>
700- 4,000	<i>Sadleria cyatheoides</i>
800- 1,800	<i>Microlepia strigosa</i>
800- 9,000	<i>Pteridium aquilinum</i>
1,000- 2,000	<i>Athyrium proliferum</i>
1,000- 2,500	<i>Polypodium Hillebrandii</i>
1,000- 4,000	<i>Dryopteris crinalis</i>
1,000- 5,000	<i>Botrychium subbifoliatum</i>
1,000- 6,000	<i>Cibotium Chamissoi</i>
1,500- 3,000	<i>Marattia Douglassii</i>
1,500- 4,000	<i>Trichomanes parvulum</i> , <i>Elaphoglossum reticulatum</i>
1,500- 4,500	<i>Dryopteris acutidens</i>
1,500- 6,000	<i>Asplenium rhomboideum</i>
1,800- 3,000	<i>Pteris excelsa</i> , <i>Doodya Kunthiana</i>
1,800- 6,000	<i>Polypodium pellucidum</i>
2,000- 3,000	<i>Elaphoglossum gorgonium</i> , <i>Dryopteris latifrons</i>
2,000- 4,000	<i>Elaphoglossum hirtum</i> , <i>Dicranopteris glauca</i>
2,000- 6,000	<i>Polypodium tripinnatifidum</i> , <i>Asplenium rhipidoneuron</i>
2,500- 4,000	<i>Lycopodium venustulum</i>
2,500- 7,500	<i>Lycopodium serratum</i>
3,000- 4,000	<i>Diellia erecta</i> , <i>Polypodium pumilum</i>
3,000- 5,000	<i>Polypodium abietinum</i> , <i>Schizaea robusta</i>
3,000- 6,000	<i>Elaphoglossum æmulum</i> , <i>Polypodium hymenophylloides</i>
4,000- 5,000	<i>Dryopteris globulifera</i>
4,000-10,000	<i>Asplenium adiantum-nigrum</i>
5,000- 6,000	<i>Dryopteris parvula</i> , <i>Lycopodium erubescens</i>
5,000- 8,000	<i>Pellaea ternifolia</i>
6,000- 9,000	<i>Polystichum sqq.</i>

I. OPHIOGLOSSALES, *Ophioglossaceæ*.

A family of 3 genera and about 50 species, of general distribution.

1. OPHIOGLOSSUM.

A genus of about 30 species, of wide distribution; both terrestrial and epiphytic.

1. *O. NUDICAULE* Lf. Recorded from Maui and Hawaii only; widely distributed in tropical and sub-tropical America, West Africa, India, and the South Pacific.

*2. *O. CONCINNUM* Brack. Recorded from Oahu and Maui, appearing after rains; often near the sea-shore; endemic.

3. *O. VULGATUM* L. All islands, 500-6000 ft, hygrophytic; wide range over the Old World, Australia and temperate N. America.

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4. *O. PENDULUM* L. All islands, epidendrous, in the rain-forests, common; widely distributed from Madagascar through tropical Asia and Australia to Polynesia.

SUMMARY. It is probable that all the species occur on all the islands, although evidently more abundant from Kauai to Maui. Altitudinal range from sea-level to 6000 ft or more. Hygro- to mesophytic. One endemic species, the others wide-ranging. All the forms are closely related.

2. BOTRYCHIUM.

A genus of about 20 species, mostly in the Northern Hemisphere, a few forms in Australasia; terrestrial.

*5. *B. SUBBIFOLIATUM* Brack. Rare, on the ground in deep, wet forests of all the islands; strongly hygrophytic; 1000-5000 ft; endemic.

The third genus, *Helminthostachys*, has but one species, which extends from the Himalayas to tropical Australia.

II. MARATTIALES, Marattiaceæ.

A family of 5 genera: *Angiopteris*, 20-30 species, Himalayas to Madagascar and Polynesia; *Archangiopteris*, 1 species, China; *Marattia*, *Kaulfussia*, 1 species, S. Asia and Malaysia; *Danaa*, 14 species, tropical America.

3. MARATTIA.

A genus of 10 or more species, ranging throughout the tropics of the world.

*6. *M. DOUGLASSII* (Presl) Baker. Fairly common in moist, shady localities on all the islands, 1500-3000 ft; hygrophytic; endemic.

III. FILICALES.

1. Hymenophyllaceæ.

A family of 2 genera and about 200 species, in damp, shady forests throughout the tropics, and in New Zealand. One species reaches central Europe, and another, Kentucky.

4. TRICHOMANES.

A genus of about 100 species, chiefly in the tropical zone and damp localities of the south temperate zone.

7. *T. BAUERIANUM* Endl. Terrestrial, in moist shady forests of all the islands; also in Polynesia and Malaysia.

8. *T. PARVULUM* Poir. On trees and rocks, all islands, 1500-4000 ft, not common; widely distributed in Polynesia, Australasia, Ceylon and Madagascar.

9. *T. HUMILE* Forst. On tree-trunks and rocks, in moist woods, all islands, not common; also in Polynesia, Java, Formosa, New Zealand and Australia.

*10. *T. CYRTOTHECA* Hillebd. Recorded only from Oahu and Maui, above 1800 ft, in the rain-forests; endemic.

11. *T. RADICANS* Sw. Common in the rain-forests of all the islands, above 2000 ft; in many tropical countries, also Ireland, Wales, west Scotland, and southern U.S. to Kentucky.

SUMMARY. The non-endemic species occur on all the islands; altitudinal range 1200–5000 ft (higher in some places). Strongly hygrophytic. One endemic species.

5. HYMENOPHYLLUM.

A genus of about 100 species; distribution as for *Trichomanes*.

*12. *H. BALDWINII* Eaton. Precinctive; collected on trees in the rain-forests above 2500 ft; endemic to Kóolau Mountains, Oahu.

*13. *H. RECURVUM* Gaud. Common, on trees in the rain-forests above 1800 ft, also on wet rocks; endemic.

14. *H. OBTUSUM* Hook. and Arn. Somewhat rare, on trees in the rain-forests, 1500–5000 ft; also occurs in New Guinea, and Cape of Good Hope.

*15. *H. LANCEOLATUM* Gaud. Rare; all islands, on trees in the montane rain-forests; endemic.

SUMMARY. 3 species occur on all the islands; the fourth is highly precinctive. Altitudinal range 1200–6000 ft; strongly hygrophytic. 3 endemic species.

2. Cyatheaceæ.

A family of 7 genera and about 300 species, widely distributed through the tropics, and far south in the southern hemisphere. The genera are: *Balanium*, 3 species; *Dicksonia*, 12; *Cibotium*, 6–8; *Thyrsopteris*, 1; *Cyathea*, 115; *Hemitelia*, 44; and *Alsophila*, 112.

6. CIBOTIUM.

A genus of remarkable distribution: 3 species in Central America, 2 in Malaya and 3 in the Hawaiian Islands.

*16. *C. CHAMISSOI* Kaulf. All islands, 1000–6000 ft, common in humid regions; endemic.

*17. *C. MENZIESII* Hook. All islands, 1000–5000 ft, not as common as the preceding, more hygrophytic; endemic. A stately tree.

*18. *C. GLAUCUM* Hook. and Arn. All islands, 1000–3000 ft, rare, hygrophytic, endemic.

SUMMARY. The 3 species are all endemic, and occur in the rain-forests of all the islands, ranging from 1000–6000 ft, sometimes lower.

3. Polypodiaceæ.

A very large and widely distributed family of about 100 genera and 4000 species. The larger genera are *Dryopteris*, 450 species; *Polypodium*, 200; *Asplenium*, 150–200; *Elaphoglossum*, 80–100; *Adiantum*, 80; *Pteris*, *Blechnum*, *Polystichum* and *Aspidium* with 50–70 each.

7. ELAPHOGLOSSUM.

A genus, mostly tropical, of 80–100 species, on rocks or epiphytic; widely distributed in tropical and sub-tropical America, Africa, South Atlantic Islands, Malaya, etc.

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19. *E. HIRTUM* (Sw.) C. Chr. Common, all islands, exposed ridges at 2000–4000 ft; also along streams in the rain-forests; occurs in many tropical countries.

*20. *E. MICRADENIUM* (Fee) Moore. Common, all islands, on rocks and trees in the rain-forests, 1000–3000 ft; endemic.

21. *E. ÆMULUM* (Kaulf.) Brack. On trees, 3000–6000 ft, also occurs in tropical America, Africa, India, Malaya, Australia.

*22. *E. WAWRÆ* (Lueresen) C. Chr. In forests and on dry shaded rocks at about 4000 ft; common on all the islands; endemic.

*23. *E. RETICULATUM* (Kaulf.) Gaud. Common, all islands, on tree-trunks and rocks, 1500–4000 ft; endemic.

24. *E. GORGONIUM* (Kaulf.) Brack. On the ground, on the roots of trees and on rotten trunks, all islands, in the rain-forests, 2000–3000 ft, also occurs in Tahiti.

*25. *E. FAURIEI* Copeland. Collected at Pukoo, Molokái, at 1800 ft; endemic.

*26. *E. CRASSICAULE* Copeland. Collected on Kauái; endemic.

*27. *E. ROCKII* Copeland. Collected at Punalúu, Kóolau Mountains, Oahu, in the rain-forest; endemic.

SUMMARY. 6 of the 9 species occur on all the islands; 3 are known only from single islands, Kauái, Oahu and Molokái. Altitudinal range 1000–6000 ft. Strongly hygrophytic. 6 species are endemic; 2 others are cosmopolitan, and the other occurs also in the South Pacific.

8. PTERIS.

A genus of 60 or more species, in all warm and tropical regions; most abundant in E. Asia, Malaya and Melanesia; mostly on stones, etc., in moist woodlands.

28. *P. EXCELSA* Gaud. Common, on all islands, in damp gulches at 1800–3000 ft, often with *irregularis*; also occurs in N. India, Malaya and Fiji.

29. *P. CRETICA* L. Common, on all islands, on ground and trees; occurs throughout the tropics and sub-tropics.

*29a. var. *DECURRENS* Hillebd. Recorded from Oahu and W. Maui; endemic.

*30. *P. IRREGULARIS* Kaulf. Fairly common, all islands; in forests and deep gulches, 1000–3000 ft, hygrophytic; endemic.

*31. *P. HILLEBRANDI* Copeland. Recorded from Kauái and East Maui, in hygrophytic and semi-hygrophytic situations; endemic.

32. *P. LONGIFOLIA* L. Collected at Wailuku, Maui; a cosmopolitan species.

SUMMARY. It is likely that all the species occur on all the larger islands. 2 species and 1 variety are endemic. The altitudinal range is 1000–3500 ft; mostly hygrophytic, sometimes mesophytic.

9. PTERIDIUM.

A monotypic genus of 1 cosmopolitan species, which with its varieties occurs throughout the north temperate zone, from the arctics to the tropics.

33. *P. AQUILINUM* (L.) Kuhn. Common on all islands from 800–9000 ft. in some places—Kea and Loa—even higher; great variability as to stature.

10. PELLÆA.

A xerophytic genus of about 55 species, of wide geographic distribution, chiefly in Africa, Andean America, Malaya and Melanesia; usually found upon rocks.

34. *P. TERNIFOLIA* (Cav.) Link. Common, all islands, 5000–8000 ft; sometimes at lower levels, in dry, exposed places; ranges over the high Andes from Chili north to Texas.

11. HISTIOPTERIS.

A monotypic genus widely distributed over the tropics and southern hemisphere, Australasia, Polynesia, etc.

*35. *H. INCISA* (Thunb.) Ag. Reported only by Hillebrand, rare; Waianae Range, Oahu; endemic.

12. DORYOPTERIS.

A genus of about 20 species, mostly in tropical America and Africa, some Malayan, some cosmopolitan in the tropics.

*36. *D. DECIPIENS* (Hook.) J. Sm. All islands, common, on rocks and along streamways, at 1000 ft and above; endemic.

*37. *D. DECORA* Brack. All islands, on exposed rocks at about 2000 ft on the dry lava fields of Kona and Ka-u, Hawaïi; endemic.

13. ADIANTUM.

A genus of 80–90 species, throughout the tropics, but most abundant in tropical America; a few in the temperate zones. Delicate ferns, inhabiting moist, shady localities, often on wet cliffs.

38. *A. CAPILLUS-VENERIS* L. Common, all islands, on ground or wet rocks, particularly in humid ravines; common in many tropical and temperate regions.

39. *A. CUNEATUM* L. and F. Collected at Kealia, Kauái; cosmopolitan.

14. HYPOLEPIS.

A genus of about 12 species, widely distributed in all warm countries.

40. *H. PUNCTATA* (Thunb.) Mett. Summit swamps of Oahu, Molokái, and West Maui; strongly hygrophytic; also occurs in Japan, China, Malaya, Australasia and Polynesia.

*41. *H. FLACCIDA* (Hillebd) Robinson. Locality uncertain, probably as for *punctata*; endemic.

15. SCHIZOSTEGE.

A small genus of 1 Hawaïian and 2 Philippine species; resembles *Cheilanthes*.

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*42. *S. LYDGATEI* (Bak.) Hillebd. In the rain-forests, near waterfalls; strongly hygrophytic; Oahu and West Maui; endemic.

16. *DIELLIA*.

An endemic Hawaiian genus of at least 8 species, with numerous varieties. As Hillebrand states, the species form a connected group, highly interesting as it exhibits a twofold line of development, from simple to very complex pinnae.

*43. *D. CENTRIFOLIA* (Hillebd) Robinson. Known only from Kauái.

*44. *D. PUMILA* Brack. On exposed cliffs, Oahu only; rare.

*45. *D. ERECTA* Brack. Kauái to Maui, 3000-4000 ft; uncommon.

*46. *D. ALEXANDRI* (Hillebd) Diels. Kauái and East Maui only; several varieties of uncertain status.

*47. *D. FALCATA* Brack. Dry, open summit ridges, Oahu and West Maui.

*48. *D. LACINIATA* (Hillebd) Robinson. Known only from Kauái.

*49. *D. KNUDSENII* (Hillebd) Diels. Known only from Kauái.

*50. *D. MANNII* (Hillebd.) Robinson. Known only from Kauái; 2000-3000 ft.

SUMMARY. It is significant that 4 of the 8 species are known only from Kauái; 2 others occur on Kauái and Maui; 1 on Oahu only; and 1 on Oahu and Maui. None are known from Hawaii; the apparent absence from Molokái may be due to lack of exploration. The habitats range from semi-xerophytic situations to the rain-forest, most abundant in the latter. Altitudinal ranges are from 1800-4500 ft.

17. *ODONTOLOMA*.

A genus of about 30 species, widely distributed in the tropics; about one-third of the species American, the remainder in Malayan and other tropical regions.

*51. *O. MACRAEANUM* (Hook. and Arn.) Brack. Common on all the islands; wide-creeping on trees in the rain-forests; endemic.

18. *NEPHROLEPIS*.

A genus of about 10 species, terrestrial or epiphytic, mostly in the tropics; some in the W. Pacific sub-tropics.

52. *N. CORDIFOLIA* (L.) Presl. On ground and on trees; in many tropical countries, Japan and New Zealand.

53. *N. EXALTATA* (L.) Schott. Very common epiphyte on trees, in the lower and middle forest zones; common in many tropical countries.

19. *ODONTOSORIA*.

A genus of about 10 species, extending from Madagascar through Asia to Japan and Polynesia; some species in tropical America and West Indies.

54. *O. CHINENSIS* J. Sm. An exceedingly common fern, on all the islands, 500-5000 ft, sometimes higher; also abundant in many tropical countries.

20. MICROLEPIA.

A genus of 10 species, 1 widely distributed throughout the tropics and subtropics, the others in Polynesia and South-eastern Asia.

55. *M. STRIGOSA* (Thunb.) Presl. Abundant on all the islands, on the outskirts and in open glades of the lower forest zone, 800–18000 ft; common in many warm countries.

56. *M. SPELUNCÆ* Moore. Not common, but apparently on all the islands; also in many warm countries.

21. VITTARIA.

A genus of 10–20 species, epiphytic in tropical forests.

57. *V. RIGIDA* Kaulf. Common on trees and rocks in the lower and middle forest zones, all islands; occurs throughout Polynesia.

22. FILIX.

A genus of 5 or more species, delicate rock ferns, mostly in temperate and boreal regions; several tropical.

*58. *F. DOUGLASHI* (Hook.) Robinson. Recorded from Hawaïi, Oahu and Maui; rare; in the rain-forests and up to 6000 ft; endemic.

23. CEROPTERIS.

A genus of about 20 species, mostly in tropical S. America; several polymorphic forms in the high Andes; several in S. Africa.

59. *C. OCHRACEA* (Presl) Robinson. Common on all the islands, in moist places; also in tropical America, Costa Rica and Natal.

60. *C. CALOMELANOS* (L.) Link. Common in moist open places, all islands, also in the West Indies and S. America.

24. CONIOGRAMME.

A genus of 2 or more species, quite variable; native to the tropics of Asia and the Pacific.

61. *C. FRAXINEA* (Don) Diels. Terrestrial, in moist places in the lower and middle forest zones, all islands, 1500–4000 ft; also in China, Japan, and other regions.

25. DRYOPTERIS.

A large and diversified genus of about 350 species, of wide geographic distribution.

*62. *D. GLOBULIFERA* (Brack.) Kuntze. All islands at elevations of 4000–5000 ft; strongly hygrophytic; endemic.

63. *D. PALEACEA* (Sw.) Robinson. Fairly common on the higher parts of Kauaï, E. Maui and Hawaïi; also occurs from Mexico to Peru.

*64. *D. FUSCO-ATRA* (Hillebd.) Robinson. Summit regions of Kauaï, Molokai, Maui and Hawaïi; endemic.

*65. *D. NUDA* Underwood. Fairly common in the lower and middle forest zones of all the islands; hygrophytic; endemic.

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*66. *D. GLABRA* (Brack.) Kuntze. All islands, at high altitudes, 4000–5000 ft; endemic.

*67. *D. PARVULA* Robinson. Kauái only, 5000–6000 ft; hygrophytic; endemic.

*68. *D. LATIFRONS* (Brack.) Kuntze. Fairly common, all islands, 2000–3000 ft, in the rain-forests, hygrophytic; endemic.

69. *D. SQUAMIGERA* (Hook. and Arn.) Kuntze. Somewhat rare, Kauái to Maui, 1800–4000 ft; also in Fiji and Tahiti.

*70. *D. HAWAIIENSIS* (Hillebd) Robinson. Summit bogs and upper rain-forests, all islands; Mauna Kea at 4000–5000 ft; endemic.

*71. *D. RUBIGINOSA* (Brack.) Kuntze. On all islands at elevations of 3000–4500 ft; strongly hygrophytic; endemic.

*72. *D. HONOLULENSIS* (Hook.) C. Chr. On all islands at elevations of 2000–4000 ft, in the rain-forests; endemic.

*73. *D. CRINALIS* (Hook. and Arn.) C. Chr. Fairly common, all islands, in the rain-forests at 1000–4000 ft; endemic.

*74. *D. KERAUDRENIANA* (Gaud.) C. Chr. Occurs in the forests of all the islands, most abundant in the district of Hamakua, Hawaíi; of indefinite growth, sustaining its “extraordinary length by means of the circinnate tips which twine around the branches of neighbouring trees or shrubs.” Endemic.

*75. *D. RUBIFORMIS* Robinson. All islands, in open places on the mountain slopes; mesophytic; endemic; growth habit like 74.

*76. *D. ACUTIDENS* C. Chr. All islands, along streams, 1500–4500 ft, and in the rain-forests; endemic.

77. *D. UNIDENTATA* (Hook. and Arn.) C. Chr. All islands, in the rain-forests at 1800–4000 ft. Several ecological variations are common.

78. *D. SANDWICENSIS* (Hook. and Arn.) C. Chr. In the forests of all the islands, also occurs in Fiji and Pitcairn.

79. *D. PROPINQUA* (R. Br.) Gilb. Very common in lowland swamps and deserted taro-patches, all islands; also in the rain-forests to elevations of 5000 ft; common in swamps in many tropical countries.

80. *D. PARASITICA* (L.) Kuntze. All islands, in open places between 4500–5000 ft; hygrophytic; occurs in many places in the tropics and sub-tropics and New Zealand.

81. *D. CYATHEOIDES* (Kaulf.) Kuntze. Common in the lower forest zone and ravines, all islands; also in New Guinea and Sumatra.

*82. *D. STEGNOGRAMMOIDES* (Baker) C. Chr. Not common, all islands, along streams and in the forests; endemic.

83. *D. TRUNCATA* (Poir.) Kuntze. Fairly common, all islands, in the lower and middle forest zones; hygrophytic; a wide-ranging species, extending from N. India, Ceylon, Malaya and Polynesia to Brazil.

SUMMARY. Of the 21 species of *Dryopteris*, 18 may be found on all the islands; 1 is known only from Kauái; 2 have irregular distribution. 15 species

are endemic. Most of the species are notably hygrophytic, and inhabit the rain-forests from 1000-6000 ft. 8 species are confined mainly to the upper forests, above 4000 ft 3 species are cosmopolitan forms.

26. POLYPODIUM.

A cosmopolitan genus of about 200 species, including ferns of every habitat; most abundant in the tropics; many epiphytic.

84. *P. HOOKERI* Brack. All islands, epiphytic on trees, not common; occurs throughout Polynesia.

*85. *P. KNUDSENII* Hieron. Epiphytic on trees, summit regions of Kauái, 4000-5000 ft; endemic.

*86. *P. PUMILUM* Robinson. Epiphytic; summit ridges of Oahu, 3000-4000 ft; endemic.

*87. *P. PSEUDOGRAMMITIS* Brack. Very common, all islands, epiphytic on trees; endemic.

*88. *P. HAALILIOLANUM* Brack. Uncommon, all islands; epiphytic on trees at elevations above 1800 ft; endemic.

*89. *P. SAFFORDII* Maxon. Common, epiphytic on trees at elevations above 1800 ft; endemic.

*90. *P. SARMENTOSUM* Brack. Common in the rain-forests, on mossy tree-trunks, rocks, decayed logs, etc.; endemic.

*91. *P. ADENOPHORUS* Hook. and Arn. Fairly common in the rain-forests above 2000 ft; epiphytic and hanging in graceful festoons from the trunks of trees; endemic.

*92. *P. PELLUCIDUM* Kaulf. Common on all the islands, on the ground and on tree-trunks, at 1800-6000 ft. This species is extremely polymorphous, and occupies a wide range of habitats; endemic.

*93. *P. HYMENOPHYLLOIDES* Kaulf. Rare, all islands, epiphytic on trees at 3000-6000 ft elevation; endemic.

*94. *P. ABIETINUM* Eaton. Rare, all islands, epiphytic on trees in the rain-forests at 3000-5000 ft; endemic.

*95. *P. HILLEBRANDII* Hook. Rare, all islands, in the lower forests, at 1000-2500 ft; on the ground and on trees; endemic.

*96. *P. TAMARISCINUM* Kaulf. Common, all islands, in the rain-forests; on the ground and on trees; endemic.

*97. *P. TRIPINNATIFIDUM* (Gaud.) Presl. All islands, in the forests above 2000 ft; Haleakala to 6000 ft; endemic.

*98. *P. ROCKII* Copeland. In the rain-forest, Kóolau Mountains, Punalúu district, Oahu; endemic.

SUMMARY. Of the 15 species, 14 are endemic and 1 occurs throughout Polynesia. 1 species is known only from Kauái, 2 others from Oahu only. The altitudinal range is 1000-6000 ft; there are considerable variations from this range. Most of the species are epidendric and hygrophytic, and abound in the wettest parts of the rain-forests.

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(*P. PHYMATODES* L. This species does not occur in the Hawaiian Archipelago, but is very common at Palmyra Island, both epiphytic and on the ground.)

27. *PHYMATODES*.

A tropical genus of 12-15 species, mostly epiphytic.

99. *P. ELONGATA* Presl. Common, all islands, on trees and rocks in the forests; occurs in many tropical countries.

100. *P. SPECTRUM* (Kaulf.) Presl. Not common, on trees and rocks in shaded situations; also occurs in Sumatra.

28. *PHLEBODIUM*.

A small tropical and sub-tropical genus, mostly epiphytic; like *Phymatodes* this genus is often included in *Polypodium*.

101. *P. AUREUM* (L.) J. Sm. Recorded only from Kauái; on ground and on trees; also West Indies, Florida, Mexico and Brazil.

29. *POLYSTICHUM*.

A cosmopolitan genus of about 75 species, mostly coarse and rigid terrestrial forms; many polymorphic forms.

102. *P. CARVIFOLIUM* (Kuntze) C. Chr. Summit regions of Kauái, West Maui and Lanái; occurs on high plateaus of China, Japan, Polynesia and Australia.

*103. *P. HALEAKALAENSE* Brack. Rare, high mountains of Maui and Hawaií, 6000-9000 ft; endemic.

*104. *P. HILLEBRANDII* Carruth. Chiefly the high mountains of Maui and Hawaií, perhaps other islands at 3000-5000 ft; endemic.

SUMMARY. These 3 species all occupy high mountain stations and semi-xerophytic habitats.

30. *CYRTOMIUM*.

A small genus of about 10 species, distributed throughout the tropics, and in sub-tropical mountains. Often united with *Polystichum*.

*105. *C. BOYDIAE* (Eaton) Robinson. All islands, on rocky ledges along streams; endemic.

106. *C. CARYOTIDEUM* (Wall.) Presl. All islands, in the rain-forests; also in India and Polynesia.

31. *TECTARIA*.

A small tropical genus, often included in *Polystichum*.

107. *T. CICUTARIA* (L.) Robinson. All islands, common in the lower forest zone, particularly in ravines, on damp rocks; occurs throughout the tropics.

32. *NEOTTOPTERIS*.

A small genus of 10 or more species; epiphytic, with fleshy, orchid-like roots, occurring in the forests of tropical Africa, Asia, Australia and Polynesia. Often included in *Asplenium*.

108. *N. NIDUS* (L.) J. Sm. The well-known "bird's-nest fern" abundant in the lower forest zone of all the islands, up to 2000 ft, both as an epiphyte, and on the ground; widely distributed in tropical Asia, Australia, Madagascar and Polynesia. Very abundant at Palmyra, mostly terrestrial, where it forms, according to Rock, the entire undergrowth in the interior of most of the islets.

33. *ASPLENIUM*.

A large genus of 150-200 species, of world-wide distribution, most abundant in the temperate zones, but with many tropical and sub-tropical species.

109. *A. UNILATERALE* Lam. Common, all islands, on trees and rocks, in humid shaded situations; also occurs in Mauritius, China, Japan and Polynesia.

*110. *A. RHOMBOIDEUM* Brack. Mountains of Maui and Hawaï, 1500-3000 ft, Haleakala 6000 ft; endemic; closely related to Andean species.

*111. *A. LUNULATUM* Sw. Common in the lower forest zone of all islands, also in many tropical countries.

112. *A. MONANTHES* L. All islands, at elevations of 3000-6000 ft; also in S. America, N. Africa, Azores, Madeira.

113. *A. TRICHOMANES* L. On the high mountains of Maui and Hawaï, from 5000 ft upwards to the limit of vegetation; spread over the temperate regions of nearly the whole world, and the high mountain regions of many tropical countries.

*114. *A. PAVONICUM* Brack. All islands, in moist, shady forests, not common; endemic.

*115. *A. PSEUDO-FALCATUM* Hillebd. In the rain-forests of all islands, common; endemic.

*116. *A. KAULFUSSII* Schlect. In the higher rain-forests of all the islands; endemic.

*117. *A. KAUAÏENSE* (Hillebd) Robinson. Kauaï only, in the rain-forest; endemic.

*118. *A. ENATUM* Brack. Kauaï to Maui, in the rain-forests; endemic.

*119. *A. HILLEBRANDII* C. Chr. Kauaï and Oahu only, variable; in the rain-forests; endemic.

*120. *A. CONTIGUUM* Kaulf. All islands, in the rain-forests, at medium elevations; endemic.

121. *A. CAUDATUM* Forst. Kauaï to Maui; occurs in many tropical countries.

*122. *A. NITIDULUM* Hillebd. All islands, rare; in the rain-forests; endemic.

123. *A. HORRIDUM* Kaulf. All islands, common in the forests, also common in the South Pacific.

*124. *A. GLABRATUM* Robinson. Kauaï and Oahu only, in the rain-forests; endemic.

*125. *A. LOBULATUM* Mett. All islands, in the rain-forests; endemic.

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126. *A. VARIANS* Hook. and Grev. Maui and probably other islands; also occurs in Africa, Ceylon, China and Japan.

*127. *A. MACRAEI* Hook. and Grev. All islands, on the ground in open woodlands, particularly in lower zones; endemic.

*128. *A. LYDGATEI* Hillebd. Known only from Niu and Wailupe Valleys, Oahu; endemic.

*129. *A. GOLDMANNII* Underw. Known only from Oahu; endemic.

*130. *A. ACUMINATUM* Hook. and Arn. Kauái to Maui, in the rain-forests; endemic.

*131. *A. RHIPIDONEURON* Robinson. All islands, in open exposed places at 2000-6000 ft; mesophytic; endemic.

132. *A. INSITICIUM* Brack. All islands, in the rain-forests; also occurs in the Philippines and New Caledonia.

133. *A. CUNEATUM* Lam. Kauái and Maui; also in Samoa, Fiji, the Philippines, and the West Indies.

*134. *A. PARALLELUM* Baker. Known only from Niu Valley, Oahu; endemic.

*135. *A. PATENS* Kaulf. Oahu and Maui; endemic; rare.

136. *A. ADIANTUM-NIGRUM* L. Kauái, Maui and Hawaíi, at 4000-7000 ft elevation; hygrophytic; variety *beta* occurs only on high mountains of Maui and Hawaíi, 7000-10,000 ft; widely distributed throughout the tropics and sub-tropics.

*137. *A. VEXANS* Heller. Oahu only, slope of Kona-hua-nui, above Manoa; rare, in the rain-forests; endemic.

*138. *A. SCHIZOPHYLLUM* C. Chr. All islands, in the rain-forests, both on the ground and on trees; endemic.

*139. *A. SPHENOTOMUM* Hillebd. Kauái, Maui, Hawaíi, 4000-5000 ft, in high summit rain-forests, strongly hygrophytic; endemic.

*140. *A. KNUDSENII* Hillebd. Known only from Kauái, rare; endemic.

*141. *A. MEIOTOMUM* Hillebd. Known only from Niu Valley, Oahu; rare; endemic.

*142. *A. POLYODON* Forst. Collected at Olokele, Kauái and Glenwood, Hawaíi, elevation 2000 ft; endemic.

*143. *A. COOKII* Copeland. Collected at Waimea, Kauái, elevation 3500 ft; endemic.

*144. *A. SECTUM* (Hillebd) Copeland. Collected at Waimea, Kauái, and on Maui, elevation 3500 ft; endemic.

*145. *A. MIRABILE* Copeland. Collected at Keinia, Kauái, elevation 1000 ft; endemic.

*146. *A. NEPHELEPHYLLUM* Copeland. Collected at Waimea, Kauái, elevation 3500 ft; endemic.

SUMMARY. Of the 38 species represented in the islands, 27 are endemic; 11 occur also in other regions; 5 are cosmopolitan species. 22 species are

localised or precinctive; 11 occur only on a single island—Kauái or Oahu. The altitudinal range is from 800 ft up to the limit of vegetation. Some species are confined to the summit regions, but the majority are distributed through the rain-forests. The majority are strongly hygrophytic; a few are mesophytic or even xerophytic. Some species are highly polymorphic and present many intergrading forms.

34. *ATHYRIUM*.

A genus of about 25 species, almost cosmopolitan, many in the mountains of East Asia, and throughout North America.

*147. *A. DEPARIOIDES* (Brack.) C. Chr. All islands, in the rain-forests; exceedingly variable; endemic.

*148. *A. PROLIFERUM* (Kaulf.) C. Chr. All islands, humid woodlands at 1000–2000 ft; endemic.

*149. *A. POIRETIANUM* (Gaud.) Presl. All islands, in the rain-forests, 700–1000 ft, sometimes higher; endemic.

*150. *A. BALDWINI* (Hillebd) C. Chr. Kauái only, summit rain-forests, above 3500 ft; endemic.

*151. *A. ESCULENTUM* (Retz.) Copeland. Collected on Kauái; endemic.

*152. *A. MARGINALE* (Hillebd) Copeland. Oahu (2600 ft), Molokái, Hawaíi; endemic.

*153. *A. MAUIANUM* Copeland. Collected at Makawao, Maui, 2600 ft; endemic.

*154. *A. KAALAANUM* Copeland. Collected at Kaala, Kauái; endemic.

*155. *A. PSEUDOARBOREUM* (Hillebd) Copeland. Mahana Valley, Lanái, 2200 ft, in damp, shady situations; endemic.

SUMMARY. All of the Hawaíian species are endemic; 3 occur on all the islands, 3 on Kauái only, 1 on Maui only, 1 on Lanái only, and 1 from Oahu to Hawaíi. They are largely confined to the rain-forests, at elevations of 1000–4000 ft.

35. *DIPLAZIUM*.

A genus of 60–70 species, occurring throughout humid tropical and sub-tropical regions. Robinson states that the Hawaíian species of *Diplazium* form a very natural group.

*156. *D. FENZLIANUM* (Leurs.) C. Chr. Kauái to Maui, occurring only as isolated individuals in the rain-forests; endemic.

*157. *D. ARBOREUM* (Hillebd) Robinson. In very humid ravines in the rain-forests, Kauái to Molokái; very rare; endemic.

158. *D. SANDWICHIANUM* (Presl) Diels. All islands, in the rain-forests; also occurs in Peru.

36. *SADLERIA*.

An endemic Hawaíian genus of 7 or more species, well-known as a pioneer on the lava-flows.

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*159. *S. SOULEYTIANA* (Gaud.) Moore. All islands, in the dense rain-forest at elevations above 2000 ft.

*160. *S. CYATHEOIDES* Kaulf. Very common on all the islands at the lower elevations, 700–4000 ft, in both hygrophytic and xerophytic habitats. Robinson states that this species also occurs in Sumatra (?)!

*161. *S. HILLEBRANDII* (Hillebd) Robinson. All islands, in xerophytic exposed situations. This is one of the first species to establish itself upon the lava flows. It is a notably drought-resistant species.

*162. *S. POLYSTICHOIDES* (Brack.) Heller. Not common, all islands, in forests on the lower mountain slopes; often xerophytic.

*163. *S. UNISORA* (Baker) Robinson. Kauái only, on the rocky walls of the very hygrophytic summit plateau.

*164. *S. FAUIERI* Copeland. Collected in Kalihi Valley, Oahu, in the rain-forests; elevation 2000 ft.

*165. *S. RIGIDA* Copeland. Reported from the summit ridges of Wai-ale-ale, Kauái, 4500 ft, and also from the summit of Lanái; hygrophytic.

SUMMARY. 4 species occur on all the islands; 1 is known only from Kauái, 1 from Oahu, and 1 from Kauái and Lanái. The ecological range is very great, from extreme xerophytism to extreme hygrophytism. The species are most abundant in the rain-forests.

37. DOODYA.

A genus of 4–5 species, occurring in the eastern part of the Old World, from Asia to Malaya, Australasia, Melanesia and Polynesia.

*166. *D. KUNTHIANA* Gaud. All islands, common along the streamways, and in wet woods at 1800–3000 ft; endemic.

4. *Gleicheniaceæ.*

A xerophytic family of 2 genera and about 30 species, widely distributed throughout the tropics, and in the south temperate zone. 1 genus, monotypic, is confined to New Caledonia; the other is well represented in Hawaïi.

38. DICRANOPTERIS.

A genus of 25 or more species, abundant in many tropical countries, in sub-tropical East Asia, and also in moist situations in the southern hemisphere.

*167. *D. HAWAIIENSIS* (Thunb.) Underw. All islands, rare, at elevations of 3000–6000 ft; endemic.

168. *D. GLAUCA* (Thunb.) Underw. All islands, here and there at elevations of 2000–4000 ft, nowhere abundant; also occurs in Japan, China, Malaya, tropical Australia and Polynesia.

*169. *D. EMARGINATA* (Brack.) Robinson. All islands, on open mountain ridges; endemic.

170. *D. LINEARIS* (Burm.) Underw. The "Stag-horn" or *Uluhe*, forming extensive and well-nigh impenetrable thickets; all islands at 600–3000 ft, in open situations; occurs in all tropical countries.

5. Schizæaceæ.

A family of 4 genera and 70 species, mostly tropical, rare in colder regions. 1 species reaches Newfoundland. Plants of diverse form and habit.

39. SCHIZÆA.

A genus of about 20 species, mostly tropical; endemic species occur in many regions.

*171. *S. ROBUSTA* Baker. Rare, in summit bogs of Kauái, Oahu and West Maui, probably also in Molokái and Kohala, Hawaíi; at altitudes of 3000 ft and over; in swamps and on trees; occasionally in exposed situations; endemic.

40. OSMUNDACEÆ.

A family of 3 genera, not represented in the Hawaiian Islands.

6. Salviniaceæ.

A family of small, floating aquatics; 2 genera and 15 species—4 in *Azolla* and 11 in *Salvinia*. Widely distributed throughout the world, but mostly tropical.

172. *AZOLLA* sp. This form has been introduced in recent years into the lowland regions of several of the islands, particularly Oahu.

7. Marsiliaceæ.

A family of 2 genera and 60 species, inhabiting marshes or aquatic. 6 species belong to *Pilularia*, 54 to *Marsilea*. Of general distribution, but mostly tropical.

41. MARSILEA.

A genus of over 50 species, widely scattered throughout the warmer regions of the world.

*173. *M. VILLOSA* Kaulf. Lowlands of various islands, particularly Oahu; wet and marshy places, such as old taro patches, fairly common; endemic.

*174. *M. CRENULATA* Desv. Known only from Oahu; endemic.

IV. EQUISETALES.

Not represented in the Hawaiian flora.

V. LYCOPODIALES.

1. Lycopodiaceæ.

A family of 2 genera—*Phylloglossum*, 1 species in Australia, Tasmania and New Zealand; *Lycopodium*, about 100 species, scattered over all parts of the world except extremely xerophytic regions. The majority of epiphytic species are tropical; several terrestrial species extend to the Arctic Circle.

42. LYCOPODIUM.

The Hawaiian species are both epiphytic and terrestrial.

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175. *L. SERRATUM* Thunb. All islands, fairly common, on tree-trunks in the rain-forests, at 2400–7500 ft; also occurs in Japan, East Indies, India, Polynesia, Mexico. The species is notably variable.

*176. *L. ERUBESCENS* Brack. Hygrophytic regions of Kauái and East Maui, 5000–6000 ft; endemic.

*177. *L. HALEAKALAE* Brack. Hygrophytic regions on Maui, at about 500 ft; endemic.

178. *L. PHLEGMARIA* L. Known only from Maui; also occurs in Mauritius, India, Australia and Polynesia.

179. *L. CERNUUM* L. Common, all islands, in open glades and along outskirts of the forests, forming thickets; common in many tropical countries.

*180. *L. NUTANS* Brack. Rare, all islands, epiphytic on trees, 2000–3500 ft, in the rain-forests; endemic.

181. *L. PHYLLANTHUM* Hook. and Arn. Common, all islands, in the rain-forests, epidendrous, pendulous; also occurs in India, East Indies, Tahiti and Samoa.

182. *L. VOLUBILE* Forst. Collected only by Menzies, on Hawaíi, probably on Mauna Loa; occurs in the South Pacific.

*183. *L. VENUSTULUM* Gaud. All islands, not common, on summit-ridges and upper regions, 2500–4000 ft; endemic.

*184. *L. POLYTRICHOIDES* Kaulf. All islands, not common, epidendrous, at elevations of 2000–4000 ft; endemic.

SUMMARY. 5 of the 10 species are endemic. 6 species occur on all the islands; 2 are known only from Maui; 1 only from Hawaíi; 1 from Kauái and Maui. The altitudinal range is 1000–7500 ft; the species are most abundant in the rain-forests. 4 or more species are epidendrous.

2. *Psilotaceæ*.

A family of 2 genera; *Tmesipteris*, 1 species confined to Australasia, and the following.

43. *PSILOTUM*.

A small tropical and sub-tropical genus of 2 or more species, widely distributed.

185. *P. NUDUM* (L.) Griseb. Common, all islands, 500–3000 ft, both on the ground and on trees; a wide range of habitats, from xerophytic to hygrophytic, chiefly the latter; occurs in many tropical countries.

186. *P. COMPLANATUM* Sw. All islands, in the rain-forests, epidendrous; not common, also occurs in Malaya, Polynesia and the West Indies.

3. *Selaginellaceæ*.

One genus with about 500 species, widely distributed but mostly tropical. The majority are hygrophytic, but a few are xerophytic.

44. SELAGINELLA.

*187. *S. DEFLEXA* Brack. Rare, all islands, at high altitudes, in summit bogs and rain-forests, at 3000-6000 ft; in the swamps and on trees; endemic.

*188. *S. ARBUSCULA* Spring. All islands, in the rain-forests, endemic.

189. *S. MENZIESII* Spring. Fairly common, all islands, in the middle forest zone; also occurs in Fiji and Samoa.

*190. *S. SPRINGII* Gaud. All islands, in hygrophytic regions, 2000-3000 ft elevation; endemic.

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ON THE HABITATS AND FREQUENCIES OF SOME MADEIRA BRYOPHYTES

BY ELEONORA ARMITAGE.

These notes on the habitats and frequencies of some Madeira bryophytes apply only to the southern side of the island up to 4500 ft (circa 1390 m.). The data were obtained from January to March, 1909.

GEOGRAPHY AND GEOLOGY

Madeira, one of the Atlantic Islands, lies 320 miles (circa 530 km.) off the coast of Africa; Funchal, on the south, is situated in lat. $32^{\circ} 37' N.$, and long. $17^{\circ} W.$ The island is about thirty miles long and twelve broad (50×20 km.), and is the top of a huge volcanic mountain rising from the bed of the ocean which here attains a depth of 13,000 ft (3,900 m.). The gradient is extremely steep everywhere, the island rising as one mountain block, culminating in a number of peaks from 5000 to 6000 ft (circa 1540–1840 m.) high at a distance of only six miles from the sea.

The island is chiefly composed of a dark coloured basalt. Where the rock decomposes, forming the mountain soil, it is called "*cascalha*." The rock sections on the lofty sea-cliffs, some of them reaching 1900 ft sheer out of the sea, are well seen from the small steamers plying from one port to another. A much contorted arrangement of volcanic rocks is shown, coloured red, yellow, brown and purple. The rocks are seamed throughout with narrow vertical dykes of grey igneous material. The soil on the lower slopes of the island and on the volcanic hills near the coast is a very fertile tufa, called "*Pedra molle*." It is red, yellow, or deep crimson in colour and is particularly suitable for vine culture.

CLIMATIC AND EDAPHIC FACTORS.

The mountain sides are seamed with precipitous ravines. The mean annual rainfall is 30 inches (circa 75 cm.), most of it falls in the winter months; and owing to the steepness, much of the disintegrating rock and soil is yearly washed into the sea. After a few hours of heavy rain the sea is coloured red for some distance out from Funchal roadstead.

The mean winter temperature is $60^{\circ} F.$ (circa $16^{\circ} C.$).

The north and south sides of the island differ considerably in climate. Clouds laden with moisture roll up from the sea on the north and condense on the mountain tops, producing much rain on the north side. Here the population is scanty, and the vegetation is more in the primeval condition which obtained throughout the uninhabited island when it was discovered by Portuguese navigators in 1419. They named it "Madeira," Portuguese for "wood," from its forest-clad aspect. In the steep northern ravines some of the ancient indigenous forest remains, Hollies, Junipers and several trees of the Laurel type. On the south the Portuguese colonists cleared and burnt it, replanting with Oak and Sweet Chestnut. Almost all these trees have been cut down for fuel and timber work, and now on every available mountain slope the quick-growing maritime Pine (*Pinus pinaster*) is planted to supply the needs of the thickly populated south side.

During winter the rain-clouds and mists constantly roll down from the mountain tops (where snow lies for a couple of months) on to the south side, veiling the summits above 4000 ft and rendering impossible the investigation of the northern side, as the passes are very high.

BRYOPHYTE COMMUNITIES.

The distribution of the Bryophyta will be considered under the following zonal divisions:

I. *Sea-level to 1500 ft (460 m.).* There are very few bryophytes in this zone; owing to the dryness of the soil and the elaborate cultivation, every yard of land that can be is terraced and cropped with food plants; but shady walls carry a few species.

II. *1500–3000 ft (460–920 m.).* Here we have wayside and woodland species along the paths and tracks leading up to the higher region and in the afforested areas.

III. *The Ravines (Ribeiras), 1000 to 4000 ft (310–1230 m.).* Here are found some of the most interesting rock and stream-bed species, but owing to the extremely precipitous character of the sides of the ravines, the absence of tracks, and the difficulty of climbing about in them, much of these narrow gorges is inaccessible.

IV. *Open mountains, 2000–4500 ft (620–1390 m.).* The turf and rock-growing species of open drier country are met with here, also epiphytes on trees and shrubs.

In studying the following lists it will be observed that a very large proportion both of the mosses and of the liverworts are found in the fruiting condition in Madeira, this is indicated by "c. fr." after the name in mosses and "c. per." in hepatics. The usual frequency symbols are used: a.=abundant, f.=frequent, o.=occasional, r.=rare, v.r.=very rare. An asterisk preceding the name of a moss or hepatic at its first mention indicates that it had not been recorded for Madeira previously.

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I. Sea-level to 1500 feet.

(a). On damp walls, generally in shade, and on wall tops.

Mosses:

- | | |
|---|---|
| <i>Funaria hygrometrica</i> c. fr., f. | * <i>Weisia calcarea</i> v. <i>mutica</i> c. fr., r. ² |
| <i>Tortula muralis</i> c. fr., o. | * <i>Bryum erythrocarpum</i> c. fr., r. |
| * <i>Dicranella heteromalla</i> r. ¹ | <i>B. murale</i> r. |
| * <i>Weisia calcarea</i> r. | |

Hepatics:

- | | |
|--|---|
| <i>Corsinia marchantioides</i> c. per., f. | * <i>Fossombronia pusilla</i> c. per., o. |
| <i>Plagiochasma rupestre</i> c. per., f. | * <i>Frullania dilatata</i> o. |
| <i>Lunularia cruciata</i> c. per., f. | * <i>Riccia glauca</i> r. |
| <i>Marchantia polymorpha</i> o. | * <i>R. glauca</i> var. <i>ciliata</i> r. |

(b) On damp earth by road-sides.

Mosses:

- | | |
|---------------------------------------|--|
| <i>Anomobryum juliforme</i> o. | * <i>Fissidens incurvus</i> c. fr., r. |
| <i>Bryum atropurpureum</i> c. fr., o. | * <i>Brachythecium rutabulum</i> c. fr., r. |
| * <i>Dicranella canariensis</i> r. | <i>Brachymenium Philonotula</i> c. fr., v. r. ³ |

II. 1500 to 3000 feet.

(a). On shady mountain ground, mostly under oak and pine trees.

Mosses:

- | | |
|---|---|
| <i>Campylopus polytrichoides</i> c. fr. ⁴ , f. | <i>Mnium undulatum</i> o. |
| <i>Fissidens taxifolius</i> f. | <i>Polytrichum juniperinum</i> o. |
| <i>Pogonatum aloides</i> c. fr., f. | <i>Eurhynchium praelongum</i> o. |
| <i>Homalothecium sericeum</i> f. | <i>E. Stokesii</i> o. |
| <i>Brachythecium illecebrum</i> c. fr., f. | <i>E. confertum</i> c. fr., o. |
| <i>B. purum</i> f. | <i>Fissidens viridulus</i> c. fr., r. |
| <i>Hypnum cupressiforme</i> f. | <i>F. pallidicaulis</i> r. |
| <i>Campylopus fragilis</i> c. fr., o. | <i>Brachythecium rutabulum</i> c. fr., r. |
| <i>Fissidens serrulatus</i> c. fr., o. | <i>Hypnum canariense</i> r. |
| <i>Bryum Donianum</i> o. | * <i>Fissidens atlanticus</i> v. r. |

Hepatics:

- | | |
|--|--|
| <i>Corsinia marchantioides</i> c. per., f. | * <i>Lophocolea heterophylla</i> o. |
| <i>Lunularia cruciata</i> c. per., f. | <i>Scapania compacta</i> o. |
| <i>Gongylanthus ericetorum</i> f. | * <i>Madotheca laevigata</i> v. <i>Thuja</i> o. |
| <i>Saccogyna viticulosa</i> f. | <i>Anthoceros dichotomus</i> o. |
| <i>Calypogeia fissa</i> f. | * <i>Riccia commutata</i> r. |
| * <i>Aneura sinuata</i> c. per., o. | * <i>Fossombronia caespitiformis</i> c. per., r. |
| <i>Fossombronia angulosa</i> c. per., o. | <i>Marsupella emarginata</i> r. |
| <i>F. pusilla</i> c. per., o. | <i>Nardia hyalina</i> r. |
| <i>Plagiochila spinulosa</i> o. | * <i>Cephalozia bicuspidata</i> r. |
| <i>Lophocolea bidentata</i> o. | <i>Madotheca canariensis</i> r. |

¹ A form bearing peculiar red translucent bulbils, figured in (2).

² This variety is also found on the curious deposit of blown sand, known as the Fossil beds, near Caniçal.

³ This very interesting member of the Bryaceae has hitherto been met with in only two other localities, Madagascar and Usambara in Central Africa; it is known from two stations in Madeira.

⁴ Fruit extremely rare, previously only known from Portugal.

(b). In damp places by the Levadas (concreted aqueducts, bringing water for irrigation from high mountain springs).

Mosses:

Philonotis rigida c. fr., f.	Bryum gemmiparum o.
Brachythecium illecebrum f.	Polytrichum commune o.
B. purum f.	Brachythecium rivulare o.
Bryum pseudo-triquetrum o.	*Barbula cylindrica c. fr., r.

(c). On open ground and bare earth and banks.

Mosses:

Trichostomum mutabile c. fr., f.	*Pleuridium subulatum c. fr., r.
Webera Tozeri c. fr., f.	Ceratodon purpureus r.
Pogonatum aloides c. fr., f.	*Weisia crispata c. fr., r.
Weisia viridula c. fr., o.	Trichostomum crispulum c. fr., r.
Bryum argenteum o.	*T. mutabile v. littorale r.
B. alpinum v. meridionale o.	Entosthodon Templetoni c. fr., r.
Pogonatum nanum c. fr., o.	*Bryum capillare c. fr., v. r.
Pogonatum piliferum c. fr., o.	

Hepatics:

Gongylanthus ericetorum f.	Aplozia crenulata c. per., o.
Plagiochasma rupestre o.	Diplophyllum albicans c. per., o.
Lunularia cruciata o.	Anthoceros dichotomus c. per., o.
Fossombronina angulosa c. per., o.	Cephalozia bicuspidata r.
F. pusilla c. per., o.	

III. *Ravines (1000-4000 feet).*

(a). On the drier rocks.

Mosses:

Ptychomitrium nigricans c. fr., a.	Bryum canariense o.
Bartramia stricta c. fr., a.	Pleuropus sericeus o.
Philonotis rigida c. fr., a.	Hypnum cupressiforme v. filiforme o.
Ptychomitrium polyphyllum c. fr., f.	Hedwigia ciliata c. fr., r.
Anomobryum juliforme c. fr., f.	Timmiella barbula c. fr., r.
Bryum platyloma c. fr., f.	Trichostomum mutabile v. littorale r.
Anaetangium compactum o.	*T. flavovirens r.
Amphoridium curvipes c. fr., o.	Leucodon Treleasei v. latifolium c. fr., r.
Webera Tozeri c. fr., o.	*Eurhynchium circinatum r.

Hepatics:

Targionia hypophylla c. per., a.	Reboulia hemisphaerica o.
Plagiochasma rupestre c. per., f.	Frullania dilatata o.
Frullania polysticta f.	Radula Lindbergii r.
Corsinia marchantioides c. per., o.	*R. Bornmülleri r.

(b). On the wetter rocks and on stones in the streams.

Mosses:

Fissidens taxifolius f.	*Hypnum cuspidatum o.
Eucladium verticillatum v. angustifolium o.	Haplodontium Notarisii c. fr., r.
Webera Tozeri c. fr., o.	Philonotis marchica r.
Bryum canariense c. fr., o.	Hypnum riparium v. longifolium c. fr., r.
B. gemmiparum o.	

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Hepatics:

- | | |
|-----------------------------------|--------------------------|
| Fossombronia angulosa c. per., f. | Conocephalum conicum o. |
| Anthoceros dichotomus c. per., f. | Marchantia polymorpha o. |
| *Reboulia hemisphaerica o. | |

IV. *Open mountains* (2000–4500 feet).

(a). *On the open turf stretches.*

Mosses:

- | | |
|--------------------------------------|---------------------------------------|
| Racomitrium heterostichum c. fr., a. | Homalothecium sericeum o. |
| Brachythecium illecebrum c. fr., f. | Brachythecium purum o. |
| Hypnum cupressiforme f. | Eurhynchium Stokesii o. |
| Polytrichum juniperinum c. fr., o. | Hypnum cupressiforme v. ericetorum r. |
| P. commune o. | H. canariense r. |

(b). *On mountain rocks and bare open ground.*

Mosses:

- | | |
|--------------------------------------|---|
| Racomitrium heterostichum c. fr., a. | Racomitrium aciculare c. fr., o. |
| Grimmia trichophylla o. | Hypnum cupressiforme v. filiforme r. |
| *G. azorica o. | Racomitrium canescens v. ericoides r. |
| Bryum alpinum v. meridionale o. | *Grimmia trichophylla v. meridionalis v. r. |

Hepatics:

- | | |
|-----------------------------------|--------------------|
| Aplozia crenulata c. per., o. | Madotheca Thuja r. |
| Diplophyllum albicans c. per., o. | |

(c). *Epiphytes.*

Mosses; on Laurus Canariensis:

- | | |
|--------------------------------------|--------------------------------------|
| Ptychomitrium polyphyllum c. fr., o. | *Orthotrichum Lyellii r. |
| Ulotia calvescens c. fr., o. | Homalothecium sericeum v. Mandoni r. |

On bushes of Vaccinium maderense 3–4 feet high.

- | | |
|------------------------------|------------------------------|
| Antitrichia curtispindula f. | Ulotia calvescens c. fr., r. |
|------------------------------|------------------------------|

Hepatics: on *Quercus pedunculata*, *Radula Lindbergii* r.; on *Vaccinium maderense*, *Frullania germana* v. r.; this rare species is known only from the British Isles and the Faroe Islands. In (1) this plant was named *F. Teneriffae*.

Many of the species and most of the genera here enumerated are also found in Britain, several of them representing the southern element of our flora as found in the south-western districts of Ireland and England, and in the Channel Islands.

So far as I can ascertain, 171 species and varieties of mosses, and 76 of hepatics, are recorded altogether from Madeira. Mr H. N. Dixon pointed out to me the interesting fact that while about 80 per cent. of the mosses are also British, the remaining 20 per cent. are mostly of quite a different range. The following notes, kindly contributed by Mr Dixon for the mosses and by Mr Macvicar for the hepatics, indicate the distribution of the non-British forms in my collection from Madeira. M, Madeira, C, Canaries, A, Azores.

MOSES: only known in M., *Amphoridium curvipes*, *Haplodontium Notarisii*, *Homalothecium sericeum* v. *Mandoni*, *Leucodon Treleasei* v. *latifolium* (species found in M., C., A.). *Dicranella canariensis* M., C. *Fissidens atlanticus* M., A. *Grimmia azorica* M., C., A. *Hypnum canariense* M., C., A., Newfoundland, possibly Ireland. *Fissidens pallidicaulis* M., C., N. Italy. *Ptychomitrium nigricans* M., C., A., S. Portugal. *Brachymenium Philonotula* M., Usambara, Madagascar. *Bryum platyloma* M., C., A., Algeria. *B. alpinum* v. *meridionale* M., C., A., Portugal (Cornwall). *B. canariense* M., C., A., Portugal, Corsica. *Eucladium verticillatum* v. *angustifolium* M., C., S. Spain (species very widely distributed). *Grimmia trichophylla* v. *meridionale* M., Norway, Caucasus, Tunis, Algeria, California. *Timmiella Barbula* M., C., S. Europe, Asia Minor, Persia, Abyssinia. *Philonotis marchica* M., Mid Europe, Japan, Caucasus, Algeria, N. America. *Ulota calvescens*, known from the British and Atlantic Islands, has lately been found in Portugal.

HEPATICS: *Corsinia marchantioides* M., C., Algiers, France, Spain, Portugal, Switzerland, Italy, Corsica, Sardinia, Louisiana, Japan. *Plagiochasma rupestre* M., C., A., Spain, Portugal, Italy, Sicily, Dalmatia, Greece, Abyssinia. *Gongylanthus ericetorum* M., C., Algiers, Spain, Portugal, France, Corsica, Italy, Dalmatia. *Madotheca canariensis* M., C., Portugal. *Radula Bornmülleri* M., C. *Frullania polystriata* M., C., A.

The thick-tissued frondose hepatic genera, *Corsinia*, *Targionia*, *Plagiochasma*, *Reboulia*, and dry, tufted mosses such as *Grimmiae*, *Rhacomitria*, *Ptychomitria* and some *Trichostoma*, are the dwellers on arid rock; on the open uplands the grey cushions of *Rhacomitrium heterostichum* are very striking from the excessive development of the long white hair-point of the leaves, useful in checking transpiration; *Haplodontium* and several *Brya* are found on the moist shaded rocks in ravines; *Bartramia stricta* and *Targionia hypophylla* were found on dry basaltic rocks in close proximity, just as in this country they grow together (in Radnorshire for instance) in like conditions; the epiphytic species are noteworthy on the infrequent arboreal and fruticose vegetation of the higher mountain slopes; while the distribution of the other forms of mosses and of the foliose and some frondose hepatics closely follows that with which we are familiar here, in woodland and wayside habitats.

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ON THE RARITY OF CERTAIN HEATH PLANTS IN BRECKLAND

By HAROLD JEFFREYS.

The heathland in the north-west of Suffolk is well known to be abnormal among English heaths in certain of its environmental relations, the most striking of these being the extraordinary severity of the biotic attack, the friability of the soil, and the extensive wind erosion¹. At the same time the flora is somewhat peculiar, several plants occurring which do not grow on heaths elsewhere in England, while on the other hand certain plants that are generally distributed on heaths in other parts of the country are absent or rare in Breckland. Two of these, *Deschampsia flexuosa* and *Agrostis canina*, are mentioned by Tansley². *Nardus stricta*, the principal dominant on grass heaths in Northumberland and Durham, is also extremely rare if not totally absent. It was thought desirable to investigate experimentally whether these facts were due to some specific quality in the environment; or whether the plants considered had merely never been introduced and would be quite capable of holding their own when they had once appeared³. For this purpose six clumps of *Nardus* and *Deschampsia* were brought from Waldrige Fell, in the county of Durham, and transplanted to a typical Breckland heath at Cavenham. *Agrostis canina* was not considered, both because it is at best of somewhat local occurrence, being absent in particular from the north-east Durham heaths, and because even where it occurs it is never dominant, whereas the other two grasses are dominant over considerable areas.

The specimens were transported with due precaution against wilting on the journey, and the original soil was retained. Further precautions were needed in planting them, for it was known from observations in the north that these plants are both attractive to rabbits, and if attacked by them before becoming well established they might be pulled up bodily⁴. They were therefore planted in pairs in wire cages in different parts of the heath, and it was intended that if the plants became established when protected, the cages should then be altered so that one clump in each was exposed to the attack,

¹ E. P. Farrow, this JOURNAL, 1915 et seq.

² *Types of British Vegetation*, p. 97.

³ W. M. Hind, in *The Flora of Suffolk*, 1889, records *Nardus* from Mildenhall and Tuddenham, but I have not seen it on any heath near. *Deschampsia* is not recorded from the vicinity.

⁴ *Juncus squarrosus*, transplanted without protection into a rabbit-attacked region at Waldrige, was not pulled up, though attacked, and established itself. The heavier attack at Cavenham, however, increased the need for protection.

the remaining clumps remaining protected and serving as controls. The netting employed was of one-inch mesh, and each cage was made in three pieces, two forming two opposite sides, while the other two sides and the top were in another piece. The advantage of this construction was that when it was necessary to expose half of the cage, it could be done easily by cutting the long strip and folding it so as to make a new side. Three cages were erected on April 9th, 1915, one being on the dry grass heath, one in a fairly open place surrounded by bracken, and the third in a swampy area dominated by *Agrostis alba*. Care was taken that each contained two pieces of both *Nardus* and *Deschampsia*.

In the cage on the dry grass heath neither of the introduced grasses produced leaves or flowers again. Their death was not due to a change in the solid constituents of the soil, for they were on the same soil on which they were well established at Walldridge; it was therefore concluded that it was caused by some change in the climate or the ground water, reduction of water being the most likely cause in view of the dryness of the locality. During the summer it was noticed that *Agrostis vulgaris* and *Festuca ovina*, the co-dominants on the grass-heath, flowered freely inside the cage, but not outside. At the same time the *Agrostis* leaves near the dead *Nardus* clumps were broad and fully three times their length in other parts of the cage: the difference may be attributed to the reduction of evaporation by the presence of the *Nardus* straw, or perhaps to nutrient matter introduced with it. The effect of dead *Agrostis* leaves in increasing the size of new stems and leaves, observed in the experiments of E. P. Farrow, indicates that the former explanation is adequate.

In the cage among the bracken, five fronds appeared during the first summer, two being well grown and three small. The latter grew up later in the summer. The herbage around the cage was very sparse and heavily attacked by rabbits; but inside it *Agrostis vulgaris* leaves attained a length of eight inches and *Festuca ovina* six inches. Both were growing very strongly.

The *Nardus* in one clump produced a few leaves; otherwise neither it nor the *Deschampsia* showed any sign of life. Even this clump did not survive till the next summer. The conditions here also were therefore physiologically unsuited to these plants. This is somewhat remarkable, as *Deschampsia* is the usual sub-dominant among sparse *Pteris* in the north of England¹; some new factor is indicated. Possibly the shallow roots of the plants from the fairly compact coal-measure sandstone soils were unable in the dry spring of 1915 to reach an adequate supply of water; yet downward growth in the friable soil of Cavenham is usually rapid, and further evidence is needed before the cause of the failure of *Deschampsia flexuosa* can be determined.

In 1916 only one bracken plant appeared in this cage. It succeeded in piercing the wire at the top, and grew to a height of eight inches above it. The cage was packed with a dense growth of *Agrostis vulgaris* and *Festuca ovina*,

¹ Cf. this JOURNAL, 4, 1916, pp. 174-195; 5, 1917, pp. 129-154.

and there was no sign of the introduced plants. The next year the bracken had disappeared. As the principal cause of the spreading of bracken over the grass heath is the rabbit attack, the natural suggestion is that the removal of this cause had reversed the advantage in competition formerly held by the bracken. Yet competition between the aerial parts did not cause the defeat of the bracken, for it always overtopped its competitors. Root competition therefore seems more likely. Had the bracken disappeared the first year, it might be thought that in the erection of the cage its rhizomes had been destroyed; but the fact that it reappeared in the first year and did not finally disappear till the third shows that this was not the cause.

The most interesting results were given by the cage on the wet agrostetum. The dominant over most of this is *Agrostis alba*, which is always eaten short by rabbits. Mixed with this are clumps of *Erica tetralix*, within which plants of *Molinia coerulea* grow. The water table when the transplantation was carried out was two inches below the surface, whereas in the other areas it was very much deeper, certainly some feet below. The ground was never submerged for long periods, so that *Nardus* would not be destroyed in this way¹. The water is brown, humous and acid, and is drained away by a small stream some yards off. In the cage situated on this the *Nardus* established itself quickly. On June 12th it was in full flower, some spikes projecting a height of three inches above the top of the cage. A week later these tall stems had been eaten off level with the top. Many shorter ones however did not reach the top, and fruit was produced in due course. On October 18th the cage was altered so that half of it was exposed to rabbit attack, the other half remaining protected. A week later there had been no change in the appearance of the vegetation, but in three weeks it was eaten short, showing that rabbits may delay for some time before making use of a newly available source of food. The clump of *Nardus* was destroyed, and has shown no further sign of life. In the protected part it is still holding its own (1918) but does not seem to be spreading, and no seedlings are visible. Some leaves of *Deschampsia flexuosa* appeared during the first summer, but it did not flower and did not survive till the next year. It is likely, therefore, that *Nardus* might be able to hold its own on the wet ground in the absence of rabbits; while their abundance at Cavenham affords an adequate reason for the absence of this grass. *Deschampsia flexuosa* is not suited to the conditions of these localities.

Meanwhile changes were taking place in the original vegetation within the cage. *Erica tetralix* is not usually attacked by rabbits, and accordingly it was not perceptibly affected by enclosure. On the other hand the other dominant, *Agrostis alba*, grew much ranker and closer in the cage than outside. Its leaves in June 1915 were three inches long inside, whereas those outside attained only one inch. A month later it had nearly filled the cage, growing quite as high as the *Erica*. After half the cage was exposed, it was there soon eaten

¹ Cf. this JOURNAL, 5, 1917, pp. 134-5.

short, forming a lawn-like carpet similar to its original state. The change of height produced by enclosure was not due to the diminution of transpiration, for a very slight wind caused the stems to vibrate inside the cage, showing that the passage of air through it was practically unimpeded. The whole of the alteration may be attributed to rabbit attack. The associated plants also underwent certain modifications. *Scirpus setaceus* appeared and flowered, though it is very rarely seen in normal conditions at Cavenham. *Radiola millegrana* and *Anagallis tenella*, both previously present, increased much in quantity, the latter adopting a suberect habit on account of the height of the surrounding *Agrostis*. *Poa annua*, *P. pratensis*, *Festuca ovina*, *Lotus major* and *Juncus bufonius* also flowered within the cage, though none of them did so outside.

It may be mentioned that so far as the appearance of the ground water and the conditions of drainage are concerned the area where this experiment was carried out closely resembles certain places at Waldrige, which are dominated by *Molinia* and *Carex goodenowii*. Both of these plants are attractive to rabbits; and it is probable that biotic attack is the cause of their limited distribution at Cavenham. Eight of the associated species mentioned by Farrow occur also in the Molinietum at Waldrige, which confirms the suggested relation between the two associations. *Erica tetralix* and *Agrostis alba* are probably selected from the normal vegetation of this type of soil to become the dominants on rabbit-infested ground, the former on account of its unattractiveness and the latter on account of its readiness to adopt a low habit and form a carpet.

SUMMARY.

On the two drier areas examined, *Nardus* and *Deschampsia flexuosa* are not capable of flourishing, probably on account of the conditions of water supply. *Nardus* could in the absence of rabbits hold its own on the damper ground, and its non-occurrence at Cavenham is caused by rabbit attack. At the same time many of the plants round the small meres are forced to become dwarf and unrecognisable, and the actual flora is probably much richer than is yet known. *Molinia* would be likely to become dominant in the absence of rabbits.

A PROPOSED CLASSIFICATION IN ANIMAL ECOLOGY

By A. B. KLUGH.

(*Queen's University, Kingston, Canada.*)

Since in animal ecology we have no such classification of habitats as that of Warming in plant ecology I venture to bring forward an outline of classification which I have used in the field for three years. I have found that this classification meets conditions as they exist in Eastern Canada, and I now bring it forward in order that it may be discussed and amended by ecologists of wider experience than myself and by those who are working in regions where habitats exist which are not represented in Eastern Canada. I shall be extremely glad to receive criticisms, suggestions and additions, and I hope, when such have been incorporated, to publish the outline in its amended form.

HYDROTHERIC FORMATION. Fresh-water.
 Intermittent Stream Association.
 Temporary Rapids Consocieties.
 Temporary Pool Consocieties.
 Permanent Pool Consocieties.
 Creniculus Association. Spring Brook.
 Potamiculus Association. Rivers and
 Creeks.
 Swift-flowing Sub-association.
 Rapids Consocieties.
 Pool Consocieties.
 Slow-flowing Sub-association.
 Silt Bottom Consocieties.
 Sandy Bottom Consocieties.
 Submerged Vegetation Consocieties.
 Limniculus Association. Lakes.
 Plankton Consocieties.
 Deep-water Consocieties.
 Stony Shore Consocieties.
 Sandy Shore Consocieties.
 Submerged Vegetation Consocieties.
 Tiphiculus Association. Ponds.
 Temporary Pond Sub-association.
 Permanent Pond Sub-association.
 Clear Bottom Consocieties.
 Chara Consocieties.
 Submerged Vegetation Consocieties.
THALASSITHERIC FORMATION. Marine.
 Pelagic Association.
 Abyssal Association.
 Littoral Association.
 Muddy Shore Consocieties.
 Sandy Shore Consocieties.
 Rocky Shore Consocieties.
 Sub-Littoral Association.
 Muddy Shore Consocieties.
 Sandy Shore Consocieties.
 Rocky Shore Consocieties.
 Tide-pool Association.

HELOTHERIC FORMATION. Marsh.
 Telmiculus Association. Fresh-water Marsh.
 Aquatic Stratum.
 Emerging Vegetation Stratum.
 Pontoheliculus Association. Salt Marsh.
HELODRIOTHERIC FORMATION. Swamp-
 Aquatic Stratum. [thicket.
 Shrub Stratum.
HYLITHERIC FORMATION. Forest.
 Black Spruce-Tamarac Association.
 Sphagnum Stratum.
 Shrub Stratum.
 Tree Stratum.
 Elm-Ash Association.
 Ground Stratum.
 Herb Stratum.
 Shrub Stratum.
 Tree-trunk Stratum.
 Maple-Beech Association.
 (Strata as above.)
 Spruce-Birch Association.
 (Strata as above.)
 Pine-Hemlock Association.
 (Strata as above.)
 Oak-Pine Association.
 (Strata as above.)
POITHERIC FORMATION. Grass-land.
 Liemonicolus Association. Moist Grass-
 land.
 Psiliculus Association. Prairie.
DRIODITHERIC FORMATION. Dry Thicket.
 Ground Stratum.
 Herb Stratum.
 Shrub Stratum.
STEIRITHERIC FORMATION. Barrens.
ACTETHERIC FORMATION. Strand.
 Amniculus Association. Sandy Strand.
 Aigiculus Association. Stony Strand.
EMEMITHERIC FORMATION. Sand.
 Thiniculus Association. Shifting Dunes.
 Amathiculus Association. Sandy Plain.

NOTICES OF PUBLICATIONS OF GENERAL BEARING

STUDIES ON SOILS AND MINERAL SALTS.

Russell, E. J. and Appleyard, A. "The atmosphere of the soil." *Journ. Agric. Science*, Vol. VII. 1915-16, p. 1.

Investigations carried out on Rothamsted soils have led to the recognition of two soil atmospheres, one, the free atmosphere occupying the pore-spaces of the upper six inches of soil, and another, of very different composition, dissolved in the surface films of water and colloids on the soil particles of the same region. The free atmosphere is similar in composition to ordinary atmospheric air, but differs from it in two respects, slightly in regard to composition and markedly in respect to constancy of constitution. It contains rather less oxygen and more carbon dioxide and nitrogen than ordinary air and is liable to periodic fluctuations of composition—especially seasonal—which are doubtless determined by the effect of corresponding fluctuations in external conditions on the activities of the microorganisms of the soil. The dissolved atmosphere, on the other hand, is almost devoid of oxygen and consists mainly of carbon-dioxide with some nitrogen. This dissolved atmosphere supplies the conditions for anaerobic life and its recognition makes it possible to conceive of anaerobic activities going on side by side with those aerobic changes common to drained cultivated soils, which we are accustomed to think of as providing essentially aerobic conditions.

Hutchinson, H. B. and McLennan, K. "Studies on the lime-requirements of certain soils." *Journ. Agric. Science*, Vol. VII. 1915-16, p. 75.

A method is described by which the degree of acidity of soils may be estimated by determining what is called by the authors the 'lime requirement,' namely, the amount of calcium bicarbonate required to render the soil water alkaline. A number of acid soils from heaths and commons apparently similar but bearing different types of vegetation were investigated by means of this method and it was found possible to classify them in terms of acidity and vegetation. It is pointed out that the conventional method of soil analysis with reference to lime content is frequently at fault and fails to give an index to observed differences in the vegetation. The method described is a simple one and is worth the attention of ecologists.

Hendrick, J. and Ogg, W. G. "Studies of a Scottish drift soil." *Journ. Agric. Science*, Vol. VII. 1915-16, p. 458.

A contrast is pointed out between the glacial drift soils of the north of Scotland composed of slightly weathered materials and those of south-eastern England, the mineral particles of which have been subjected to age-long weathering. Great caution is needed in applying conclusions based on a study of soils of the latter type to glacial drift soils of the comparatively unweathered type.

Prescott, J. A. "The phenomenon of absorption in its relation to soils." A résumé of the subject. *Journ. Agric. Science*, Vol. VIII. 1916, p. 111.

An historical review of the literature and experimental work dealing with absorption by soil of salts and colouring matters in solution. The fact of such absorption has been on record since the time of Aristotle, who noted that sea-water lost some of its taste by filtration through

sand. The acidity of certain soils has been attributed by modern workers to absorption phenomena rather than to the presence of free organic acids and there is a tendency in recent soil work to associate all soil absorptions with the general phenomena of adsorption. The part played by different soil-constituents in the various kinds of absorption observed is still unknown but it is stated by the author of this paper that "probably we are working towards a more precise definition of available plant foods based on our knowledge of how the soil absorbs them in the first instance."

Lipman, C. B., Burgess, P. S. and Klein, M. A. "Comparison of the nitrifying powers of some humid and some arid soils." *Journ. of Agric. Research*, Vol. VII. No. 2, 1917, p. 47.

It has been stated on the authority of Hilgard (1906) that nitrification is especially active in arid soils. As the result of an extended experimental study of arid soils in California the authors of the present paper reach a different conclusion, holding that there is no evidence that the nitrifying powers of soils are more intense in arid regions than they are in humid regions.

Sharp, L. T. and Hoagland, D. R. "Acidity and adsorption in soils as measured by the hydrogen electrode." *Journ. Agric. Research*, Vol. VII. No. 2, 1917, p. 123.

The authors of this paper hold that "soil acidity should not be set apart and considered as a phenomenon unrelated to the ordinary concepts of acidity." They have investigated the acidity, i.e. the H-ion concentrations, in various soil suspensions and soil extracts, using the hydrogen electrode method and an apparatus modified from that of Hildebrand (1913). Experimental data were also secured with respect to the lime requirements of soils and the so-called "adsorption of bases." They conclude that soil acidity is due to the presence of an excess of hydrogen ions in the soil solution and that direct evidence of this can be given by hydrogen-electrode measurements. Several phases of "adsorption" phenomena were studied and some general theoretical considerations bearing on the relation of adsorption to chemical reactions in soils are presented in the paper. An electrometric method for the determination of the lime requirements in soils is suggested and a convenient method described for utilizing the hydrogen electrode in soil studies.

Wyatt, F. A. "Influence of calcium and magnesium compounds on plant growth." *Journ. of Agric. Research*, Vol. VI. 1916, p. 589.

There is conflicting evidence as to the effect of compounds of these metals on plant growth under crop conditions and as to the necessity for a definite CaO/MgO ratio for optimum growth (Loew, 1892). Among other results the authors found experimentally that the crop yields and the ratio of calcium to magnesium in the plants have no direct relation to the ratio in the natural carbonates applied. They found also that different ratios of calcium to magnesium within rather wide limits produced no marked differences in yields and that all the plants grown (wheat, soy beans, alfalfa and cow peas) showed tolerance of calcium and magnesium salts.

Headley, F. B., Curtis, E. W. and Scofield, C. S. "Effect on plant growth of sodium salts in the soil." *Journ. Agric. Research*, Vol. VI. 1916, p. 857.

During the reclamation of a tract of salt land in Nevada, laboratory experiments were made to determine the degrees of tolerance of certain plants to the common salts of sodium.

The values obtained showed that the limit of tolerance is not a fixed point but is extremely variable, and that the same plant may show marked differences in tolerance at different periods of growth. The facts make the problem of reclamation of such land a very complex one.

M. C. R.

THE WATER RELATION.

Briggs, L. J. and Shantz, H. L. "Daily transpiration during the normal growth period and its correlation with the weather." *Journ. Agric. Research*, Vol. VII. No. 2, 1917, p. 155.

This paper deals with the daily transpiration of certain crop plants. Measurements were made with a view to determining: (1) the march of transpiration during the growth period, and (2) the extent to which the daily transpiration is correlated with various weather factors. The results of the research are presented in a series of graphs, but are too complex to summarise with any adequacy in a short notice.

Alway, F. A. and Clarke, V. L. "Use of two indirect methods for the determination of the hygroscopic coefficients of soils." *Journ. Agric. Research*, Vol. VII. No. 2, 1917, p. 345.

The Briggs and Shantz (1912) method for estimating the hygroscopic coefficient of soils is criticised in this paper and held to give such unreliable values in the case of certain soils that it is unsuitable for use either for studies of available soil moisture or for soil-surveys. A method is described for calculating the hygroscopic coefficient from the hygroscopic moisture found in a soil which has been allowed to come into equilibrium in a partially saturated atmosphere.

Alway, F. A. and Joubetts, C. Russell. "Use of the moisture equivalent for the indirect determination of the hygroscopic coefficient." *Journ. Agric. Research*, Vol. VI. 1916, p. 833.

A critical review of the use of the Briggs and Shantz formulae for calculating the amount of available water in soil indirectly from (a) the wilting coefficient; (b) the maximum water-capacity as defined by Hilgard; (c) mechanical soil analyses. On the basis of their own experimental work the authors judge that no general formula is universally applicable to estimations based on mechanical analyses, and also that in general the effect of considerable amounts of organic matter is to raise the value of the ratio of moisture equivalent to hygroscopic coefficient. They advise also that before employing the indirect method of calculating the hygroscopic coefficient from the moisture equivalent the ratio should be experimentally determined for each of the *types* of soil under consideration. (See Briggs and Shantz, U.S. Dept. of Agric., Bur. Plant Industry, Bull. 230, 1912.)

M. C. R.

NOTICES OF PUBLICATIONS ON BRITISH VEGETATION

Petherbridge, F. R. "Some observations on the flora and fauna of flooded fenland." *Journ. Agric. Science*, Vol. VII, 1916, p. 508.

Several thousands of acres of fenland were deeply flooded in January 1915. Some months after removal of the waters and while the land was still in a very wet condition the observations described were made on a portion of the flooded area.

In pasture land all the useful grasses had been killed and the soil throughout was slightly acid to litmus. The most striking feature was the presence over the greater part of the area of a 'mat' of *Cladophora flavescentis* and other algae and the presence of *Polygonum amphibium* in great abundance. *Chara* spp. were abundant in the neighbourhood of dykes and attention is drawn to the possibility of remains of these plants acting as a lime dressing to the soil and so neutralizing its acidity after flooding.

Stapledon, R. G. and Jenkins, T. J. "Pasture problems: indigenous plants in relation to habitat and sown species." *Journ. Agric. Science*, Vol. VIII, 1916, p. 26.

In this analytical study of the vegetation of various kinds of grass land the types considered have been classified into *natural* and *semi-natural* grasslands with further subdivision of both classes according to the botanical composition of the herbage. Various stages in the stabilisation of semi-natural grasslands—through *tended* to *untended* and thence to natural types—are recognized and described.

The paper forms an interesting contribution to the ecology of grassland and records observations of practical interest, as, for instance, the extent to which plants such as *Juncus squarrosus*, *Bellis perennis* and *Statice maritima* are relished by stock.

Another point of practical importance raised is the need for careful study of locally successful forms of *Festuca ovina* and other grasses with a view to comparison with their counterparts of commercial origin and the desirability of establishing local supplies of indigenous seed.

M. C. R.

THE ECOLOGY OF SCRUB

Salisbury, E. J. "The ecology of scrub in Hertfordshire: a study in colonisation." *Trans. Herts. Nat. Hist. Sci.* **17**, 1918, pp. 53-64.

The author regards scrub as a progressive stage in the development of forest, often maintained in the scrub-condition by factors inhibiting the development of trees, such as coppicing, grazing, burning or exposure (e.g. at the upper altitudinal limit of forest). He distinguishes *woodland scrub*, which is usually open and contains trees in an early stage of development, from *thicket scrub*, forming a closed thicket and characteristically devoid of trees. The latter is often composed of spinose shrubs, such as *Ulex*, *Prunus spinosa*, *Crataegus*, and the fruticose Rubi, and has a smaller number of herbaceous species, except at the edge, than woodland scrub. It may be suggested that the dense shade under thicket scrub inhibits the growth of tree seedlings, as of herbaceous species, and thus tends to render the thicket a permanent type.

A large proportion of the herbaceous plants of scrub are "marginal" species of the woodland (largely corresponding also with "hedgerow" plants), and others, in the case of scrub arising on what was formerly arable land, are weeds. The same composition holds of recently coppiced areas in woodland. Owing to this mixed composition the scrub associations possess a large number of species. Four areas of Hertfordshire scrub are described and listed and their relations to the natural types of woodland pointed out.

NOTICE OF PUBLICATION ON FOREIGN VEGETATION

THE VEGETATION OF A SOUTHERN SWISS VALLEY.

Bär, J. Die Vegetation des Val Onsernone (Kanton Tessin). 80 pp., with phytogeographical map. Zürich. Rascher & Co. 1918.

This description of the distribution of vegetation in a mountainous drainage basin on the borders of Switzerland and Italy a few miles north-west of the head of Lago Maggiore is published under the auspices of the admirable Phytogeographical Commission of the Swiss Naturalists' Society, which has been active in recent years in promoting and systematising surveys of Swiss vegetation. The author carried out his researches in 1905-1909 and published his results in detail four years ago¹, but with the help of the Commission the map now appears for the first time together with a general sketch of the vegetation of the district. The symbols used in the map do not, however, conform to those fixed by the Commission, because the map was completed before the Commission had carried out this work.

The region dealt with comprises an area of about 113 square kilometres, roughly the area of drainage of the Isorno, bounded by ranges of mountains exceeding 2000 m. on both north and south. The confluence of the Isorno with the Melezza, at the lower end of the area, has an elevation of 254 m. (Lago Maggiore, 200 m.) while the head of the valley is 1408 m. above the sea, and is closed in by peaks of over 2000 m.: the highest peaks of the northern watershed also exceed 2000 m., the Pizzo Rosso reaching 2548 m. The relief of the whole area is very sharp, the ground being intersected by innumerable ravines, so that there is scarcely a flat tract of ground of any size in the whole region. In spite of the moderate elevation of the mountains, the barriers to the ingress of plants are formidable. The precipitation is high, about 2000 mm. in the central valley stations, and probably exceeding 2000 mm. on the southern mountains. The great bulk of the rain falls in the period from May to October, but the number of rainy days is low and of clear days high. The winter temperatures of the valley are relatively high, the mean being round about 0° C. The climate is markedly "insubrian."

By far the greater portion of the area up to 2000 m. is covered with trees or shrubs. The general altitudinal forest zonation on northern exposures is chestnut (250-900 m.), beech (900-1100 m.), silver fir (1100-1300 m.), spruce (1300-1700 m.), larch (1700-2000 m.): on southern exposures, chestnut (250-1050 m.), beech (1050-1750 m.), larch (1750-2100 m.). Birch (*B. pendula* = *verrucosa*) and to a less extent lime (*T. cordata*), oak (*Q. sessiliflora*) and grey alder (*Alnus incana*) also form well-marked woods depending on local climatic and soil factors.

The chestnut, a typical "insubrian" tree, ranges from the lowest point of the area up to about 1000 m. in stands, and to 1200 m. as single trees. It generally follows the courses of the deep ravines where it can get protection, and at the higher levels affects southerly exposures. It occurs in the two semi-artificial types of association familiar to travellers in the valleys southward of the Alps. In the first type (*selva*) the large pollarded orchard trees stand in grassland, and from these trees the poorer inhabitants obtain most of their subsistence, chestnut meal almost entirely replacing both bread and potatoes, while the new

¹ Under the title "Die Flora des Val Onsernone" in the *Vierteljahrsschr. d. Naturf. Ges. in Zürich* (1914) and *Boll. Soc. Ticinese di Scienze Naturali* (Lugano, 1915).

shoots are cut off and dried in summer to furnish winter fodder for cattle. Secondly there are the chestnut coppices (*palina*) which are cut every seven or every ten to fifteen years the coppice wood being used for fuel and the larger stems sometimes for constructional wood. *Calluna vulgaris*, *Erica carnea*, and where pastured *Festuca capillata* are among the dominant members of the ground flora of the coppices, while the orchards are characterised by *Trisetum flavescens* and other grasses.

The beech woods range from 500 m. to 1450 m. (north) and from 1000 m. to 1850 m. (south exposure). They penetrate up the lateral ravines on the southern aspects but occupy projecting spurs on the northern aspects of the main east and west valley. The typical European associates of the beech (*Polygonatum officinale*, *P. multiflorum*, *Paris*, *Allium ursinum*) are absent, while *Convallaria*, *Maianthemum*, *Anemone nemorosa* and *Asperula odorata* are rare. The author attributes this to the recent and rapid entrance and extension of the beech in the area, an extension with which its associates have not kept pace. Beechwood is used in the valley almost entirely as firewood.

The birch (*B. pendula* = *verrucosa*) occupies mostly damp northern exposures, mainly on a humous soil poor in mineral salts, from 300 to 1400 m., while individual trees range from the mouth of the valley (250 m.) up to 1800 m. It is accompanied very characteristically by *Sarothamnus scoparius* in sunny places, also by *Calluna*, *Molinia* and *Pteridium*, often in pure communities. When birch wood is pastured, meadows of *Molinia* arise on wet and of *Bromus erectus* on dry ground, while *Festuca rubra*, *F. capillata*, *Agrostis tenuis*, *Brachypodium silvaticum* and *Luzula silvatica* also often form ground communities.

The oaks *Q. sessiliflora* and *Q. pubescens* and the lime (*T. cordata*) form less important deciduous woods or scrub. *Q. sessiliflora* occurs mostly as scattered trees up to 1400 m. *Q. pubescens* on the other hand forms communities only in warm valley basins up to 1000 m., but these are generally kept in the form of scrub by continual goat pasturing. The author remarks that the peasants show a clearer appreciation than many botanists of the distinction between these two trees, since by preference they cut the younger branches of *Q. sessiliflora* for fodder because it gives a better yield. The associates of the oak scarcely differ from those of the chestnut coppices. The lime woods occur mostly within the chestnut zone, but ascend occasionally to 1400 m. Characteristic of them are *Festuca varia*, *Poa nemoralis* and *Brachypodium silvaticum*. The lime fills up gaps in the beech and chestnut woods, colonising clefts and spurs of the often almost vertical ravine sides, the deeper soil being occupied by chestnut or beech. The ash, the aspen, the two alders (*Alnus glutinosa* and *A. incana*), *Salix grandifolia*, *Laburnum alpinum*, the mountain ash and the white beam are freely mixed in the lime woods. *Alnus incana* forms "Auenwald" on damp level ground beside streams.

Of coniferous trees *Abies alba*, *Picea excelsa* and *Larix decidua* are the most important wood formers. The silver fir forms a zone on northern exposures at 1100 to 1300 m., showing a special preference for slopes that are often covered with mist. *Rhododendron ferrugineum*, *Calamagrostis villosa*, *C. arundinacea*, and the parsley fern, the male fern, the lady fern and the broad buckler fern are characteristic constituents of its undergrowth.

The spruce forest forms an almost continuous zone on northern exposures above the silver fir zone or, where that is absent, above the beech zone. It is dominant from 1400 or 1500 m. up to 1750 m. where it passes over gradually into the larch zone. On southern exposures the spruce zone is much more interrupted, since here the beech goes higher and the larch, which begins lower, often follows directly upon it. Undergrowth is absent from close stands of spruce, and the ground flora is very sparse. *Rhododendron ferrugineum* and *Vaccinium myrtillus* are the commonest plants where the stand is more open.

The larch is the only stand-forming tree above 1600 m. on northern and 1750 m. on southern exposures, the upper limit being between 1900 and 2000 m., but the stands are often very open and scarcely deserve the name of "wood"—"pasture wood" would be more

appropriate. *Nardus stricta* and *Carex sempervirens* are the dominant plants of the herbage on southern exposures, but the wood floor is often overgrown with the dwarf juniper. On northern exposures *Rhododendron ferrugineum* with tufts of *Calamagrostis villosa*, with the addition of *Vaccinium myrtillus* accompanied by *Cetraria islandica* and *Cladonia rangiferina* on flatter ground, are characteristic. *Calamagrostis villosa* is almost the sole turf-forming grass in larch woods with alpine rose undergrowth, with *C. arundinacea* on steep slopes. The larch also grows at much lower levels, far below the upper limit of beech, on dry sunny ridges. This mingling of the continental larch with the sub-oceanic beech the author attributes to the combination of strong insolation with heavy rainfall.

The large area occupied by deciduous scrub in the valleys is mainly due to its exploitation as pasturage for goats. The "Buschweide" is used in this way all the year round, the animals feeding on the buds, small twigs and bark during the winter. It consists very largely of hazel scrub; *Corylus*, according to the author, being specially suited to colonising dry rocky soil, especially when the soil is so shallow that no trees can maintain themselves. This *Corylus* scrub is mainly intercalated between the chestnut and beech zones but also ascends to 1600 m. where the soil specially favours it. It occurs in greatest extent near villages about 800 to 1000 m. Typically it is developed on southern slopes, being much mixed with *Alnus incana* on other exposures. The grey alder more or less replaces the hazel in more shaded places but is little suited for pasturage, both because the goats will not eat it if they can get anything better and because *Brachypodium silvaticum* is the almost exclusive dominant within it. The vegetation accompanying hazel scrub is very various, both because of the great variety of minor types of habitat within the scrub, and because of the variety of exposure and altitude. *Agrostis tenuis (vulgaris)* is dominant in the pastured turf, *Festuca duriuscula*, *F. varia* and *Poa nemoralis* on rocks, but there is scarcely a meadow or wood plant of the altitudinal limits of the *Corylus*-scrub that may not be found within it. "Buschweide" of *Quercus pubescens* occurs only in the warmest basins, and the accompanying flora scarcely differs from that of the chestnut scrub. This latter is true coppice, not Buschweide, since the goats will only eat it in default of anything better, whereas they are particularly fond of the oak. The birch forms scrub on dry and more humous soils. It is more or less avoided by the goats, which dislike getting the papery bark between their teeth, and consequently tends to grow up and form trees. *Sorothamnus* and *Calhuna*, the latter sometimes dominant, particularly accompany the birch. Beech scrub comes into existence after felling of a beech wood as a transition stage back to forest, but where there is much pasturing, as in the neighbourhood of "Maiensässe" and the lower Alps, it is kept in the scrub form. Cattle as well as goats are here involved, and their trampling reduces the beech scrub to separated clumps of eaten down bushes with more or less extensive tracts of turf between. The centres of these clumps often grow up into trees. The beech appears to be spreading in spite of the heavy pasturing, no dead stumps occurring, whereas there is no lack of spruce and larch stumps. Willow scrub (*Salix purpurea* and *S. incana*) is very limited within the area on account of the absence of broad flat alluvial valleys, but the former flourishes here and there on the gravelly or sandy alluvium near the mouth of the Isorno. The accompanying vegetation is xerophilous since its roots do not reach the water table and the surface is periodically exposed to extreme drought. *Hippophaë* scrub, so characteristic of the gravelly alluvium of alpine valleys, is quite absent. The alpine alder (*Alnus viridis*) forms extensive and mostly closed associations on northerly slopes at the higher altitudes (800-1950 m.). This bush is specially adapted to snow pressure, since it grows out horizontally from the slope, and after being pressed on to the surface by the masses of snow, recovers its position when the pressure is removed. Consequently it is able to occupy avalanche tracks. It is practically inaccessible to goats on account of its growth form and is consequently little eaten. The alpine alder is frequently mixed with the alpine rose, in spite of the fact that the latter is

properly a humus plant while the former prefers soil rich in mineral salts. *Brachypodium silvaticum* occurs in the alpine alder scrub at lower, *Calamagrostis villosa* at higher levels, while *Geranium silvaticum* is a characteristic associate from the lowest to the highest levels. "Hochstauden" vegetation is indeed characteristic of alpine alder scrub.

Of "coniferous scrub," the prostrate variety of the mountain pine is confined to a single locality; dwarf juniper scrub occurs either as undergrowth of open larch woods or, above the tree limit, as an independent association on dry southern exposures, suppressing other vegetation and rendering the ground absolutely useless for pasture. The upright juniper is well distributed but does not form associations, while the yew is comparatively rare.

One of the most interesting of scrub associations is that formed by the Mediterranean *Cistus salviifolius*, which occurs at the exit of the valley at one of the warmest points of "insubrian" Switzerland. This association also occurs at Locarno, Ponte Brolla, and Ancona. The author remarks that this shrub, though it occupies the sunniest rock exposures, is not a xerophyte, but requires abundant moisture in the substratum. It is nearly always associated with *Sarothamnus* which has similar but much less exacting needs. Its other associates are an interesting mixture of warmth-loving southern and damp-loving alpine species. In Provence *Cistus salviifolius* ascends fairly high into the hills but it certainly inhabits dry soil right down to the coast. The alpine rose scrub (*Rhododendron ferrugineum*) which is abundant in the region and attains a considerable stature the author counts as forming a member of the laurel-leaved associations in spite of its small leaves. It ranges from 350 m. up to more than 2350 m. and forms very extensive associations, its greatest development being in the larch zone where it often forms the undergrowth of the woods. Above this zone it forms independent communities, and below appears in the spruce, birch and beech woods and even in chestnut scrub, mainly on damp northern exposures. Like the grey alder and dwarf juniper scrub it is useless for pasture. Holly and ivy are not common or important in the region, a fact which rather tells against the author's classification of the alpine rose as a laurel type. It is mentioned that *Rhododendron ponticum*, a true laurel type, occurs in interglacial deposits in a neighbouring valley.

To the heath type the author reckons the *Sarothamnus* association, which is very extensive in the lower part of the valley, especially on south exposures with humous soil underlain by impermeable glacial loam, and is accompanied by juniper, *Calluna*, *Pteridium* and *Brachypodium pinnatum*: *Calluna* itself, which forms independent communities as well as the undergrowth of birch and chestnut woods, and all possible transitions to grassland, at the higher levels providing poor sheep pasture: *Vaccinium myrtillus*, which at lower levels forms exclusively the undergrowth in humous fairly dry woods of chestnut and birch woods, at higher levels the undergrowth of open fir and larch woods, and above the tree limit independent communities or the undergrowth of alpine rose: *Salix herbacea*, forming thick carpets above 1800 m. and an important constituent of the "Schneetälchen" vegetation; and *Loiseleuria procumbens*, on dry humous summits. *Erica carnea*, so common on the mid-European calcareous hills, is rare and local in the area.

Of "meadow" types the author describes the "Hochstauden" vegetation, which is poorly developed but contains a great number of species. *Pteridium* occurs in enormous quantity associated with scrub, and often persists for many years after the scrub is removed, penetrating into pastures and being difficult to eradicate, as in this country. The "lairflora" is well developed but certain species are missing, probably on account of the absence of lime. The dominants of "evergreen meadows" described are *Bromus erectus*, *Brachypodium pinnatum*, *Festuca duriuscula*, *F. capillata*, *F. varia*, *Carex sempervirens*, *Nardus stricta* and *Carex curvula*; those of "Frischwiesen" (excluding manured ground) are *Carex ferruginea*, *Luzula spadicæa*, *Brachypodium silvaticum*, *Agrostis tenuis*, *Calamagrostis arundinacea*. The composition of the "Schneetälchen" vegetation is various in different places, including

Anthelia, *Polytrichum*, *Salix herbacea*, *Gnaphalium supinum*, *Alchemilla pentaphyllea*, *A. glaberrima* and *Sibbaldia procumbens*. The related "Schneefleck" flora, which differs from the former by having no drainage channel and thus an always moist substratum, and never forms a close turf, is characterised by *Ranunculus glacialis*, and includes *Soldanella pusilla*, *Oxyria digyna*, *Saxifraga Segueri*, etc. In time drainage is established and the vegetation passes over to that of the Schneetälchen. The most important types of manured meadows are dominated by *Trisetum flavescens*, *Festuca rubra*, *Agrostis tenuis*, *Cynosurus cristatus* and *Poa alpina*.

The swamp, moor and freshwater types of vegetation are relatively unimportant in the Onsernone. True "Hochmoor" is absent, owing to the conformation of the ground, though the characteristic species (*Sphagnum*, *Drosera*) occur as a result of the general poverty in mineral salts. Of "Flachmoor" species *Molinia* is the only one which dominates considerable areas at the lower levels. In the Rhynchosporetum albae *Lycopodium inundatum* has been found for the first time in the Ticino province. Other restricted "Flachmoor" dominants are *Trichophorum* (*Scirpus*) *caespitosum* and *Carex fusca* (*Goodenourii*). Various rock types, dominated by ferns, mosses and lichens are described, and also talus vegetation of different kinds. The ruderal flora is very well developed in spite of the isolation of the valley, and contains a great number of species.

The map is of the type commonly executed by the Swiss phytogeographers, which distinguishes dominants by coloured symbols and thus enables the numerous mixtures and transitions of the vegetation to be depicted. Only the woody dominants are given, and the almost complete colouring of the area gives a striking demonstration of the relatively very small extent of the herbaceous types. The cartography is exceedingly good. There is also a useful profile showing the altitudinal distribution of the dominant trees and shrubs. •

BRITISH ECOLOGICAL SOCIETY

Two Summer Meetings have been held in the present year, the first, on June 29, taking the form of an excursion to Breckland, where Dr E. P. Farrow demonstrated many of the phenomena described in his series of papers in the JOURNAL.

The chief features illustrated were the effect of rabbits on the different types of vegetation, the formation, undercutting, and final detachment of sand hummocks by the action of wind-driven sand, the destructive effects of dead bracken fronds on *Calluna vulgaris*, and the biological obstruction offered to the advance of *Carex arenaria* by a row of planted pine-trees. The excursion, which was in every way successful, was attended by eleven members and visitors.

The second meeting was held in conjunction with the 'Yorkshire Naturalists' Union at Huddersfield and Settle from Aug. 1 to Aug. 6. Its success was largely due to the excellence of the local arrangements, for which Dr Woodhead and Mr Cheetham were mainly responsible.

The programme opened with a meeting in the Biological Department of the Technical College, Huddersfield, with Dr W. G. Smith, President of the Society and President-elect of the Y.N.U., in the chair. The Chairman expressed the general gratification at the arrangement of a joint meeting of the two bodies. He then read a paper on the general characters of hill and valley vegetation in the hill regions of northern Britain, dealing especially with the grassland associations. Dr T. W. Woodhead contributed a paper on the Vegetation of the Pennine Moors, describing the character of the Wessenden and Saddleworth district of the Southern Pennines, which were to be visited next day. Dr A. Gilligan gave an account of the topography and geology of Ingleborough, to be visited later in the meeting, and Mr C. A. Cheetham dealt with the vegetation around Settle. All the papers were fully illustrated by lantern slides, and greatly added to the value and enjoyment of the excursions which followed.

On Friday the party travelled by car to Marsden and thence walked up the valley, past the series of reservoirs belonging to the Huddersfield corporation to Wessenden Head, with its great *Eriophorum* moor, *Rubus Chamæmorus* being locally prominent on partly drained peat. In descending to Saddleworth the dominance of *Molinia* was noted on slopes flushed by surface water issuing from the junction of the Millstone Grit and the underlying shale. In the evening the party travelled *via* Manchester to Settle. The next day, Saturday, was devoted to the region around Ingleborough, under the leadership of Mr Cheetham. Good examples of limestone pavement, one of the characteristic features of the district, were examined close to Ribbleshead station. The most abundant species of the characteristic cleft flora, developed in the vertical clefts arising from the master joints of the massive horizontally bedded limestone, were *Geranium robertianum*, *Scolopendrium vulgare*, *Mercurialis perennis*, *Oxalis acetosella*, *Cystopteris fragilis*, *Asplenium Trichomanes*, *A. viride*, *Allium ursinum*, *Lactuca muralis*, *Convallaria majalis*, with a certain number of shrubs such as *Crataegus oxyacantha*, *Prunus spinosa*, *Corylus avellana*, etc. Not far off, at Colt Park, a magnificent example of ash wood developed on the pavement was demonstrated to the party by Mr Cheetham. The pavement in the wood was covered with moss and herbage concealing the clefts and making the going difficult. Here a much richer flora was present, including most of the plants of the cleft flora of the open pavements, which, as will have been noticed, are largely woodland species. *Actaea spicata*, *Geranium sylvaticum*, *Campanula latifolia*, *Rubus saxatilis* and *Viola amoena* in large quantity were met with. *Prunus padus* and *Viburnum opulus* were prominent in the wood. After leaving the wood, Simon Fell was ascended and the route pursued over *Calluna* heath, with *Empetrum*, *Vaccinium myrtillus* and *V. vitis-idaea*, to Ingleborough itself, where the alpine plants *Sedum Rhodiola* and *Saxifraga stellaris* on the northern cliffs, and the summit plateau with *Festuca ovina*, *Carex rigida*, *Juncus squarrosus* and stunted *Vaccinium myrtillus*, were examined. On the return journey good examples of the belt of *Nardus* at the edge of the peat plateau, as recently described in the JOURNAL by Dr Smith, and of limestone swamp with the characteristic *Primula farinosa*, *Selaginella spinosa* and *Schoenus nigricans* were met with.

On Sunday a visit was paid to the famous Victoria Cave near Settle, where Mr Root and Dr Gilligan greatly added to the interest of the party by their lucid accounts of the history of the deposits and the mammalian and human remains. The vegetation of this neighbourhood is mainly limestone grassland with *Sesleria coerulea* and *Viola lutea*. The prevalence of typical heath species such as *Calluna vulgaris* and *Triodia decumbens* in this grassland is a noteworthy feature. Disused lead workings showed a characteristic flora like that of similar situations in Wales and Derbyshire, and including *Arenaria verna* and *Thlaspi occitanum*.

Monday and Tuesday were devoted respectively to the Keasden Beck and Austwick neighbourhoods, where the vegetation of the shales and sandstones and of the scar woods and limestone copses was examined.

The weather was consistently fine, except on the last day. The cordial thanks of the Society are due to the Yorkshire naturalists for the admirable programme and arrangements.

ANNUAL GENERAL MEETING.

The Annual General Meeting will be held on Saturday, December 21st, at University College, London.

E. J. S.

THE
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• VOLUME VII

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THE JOURNAL OF ECOLOGY



EDITED FOR THE
BRITISH ECOLOGICAL SOCIETY

BY
A. G. TANSLEY

VOLUME VII

WITH TWO PLATES AND NUMEROUS FIGURES
IN THE TEXT



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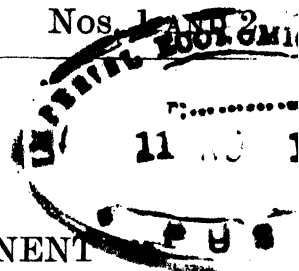
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THE ISLAND AND THE CONTINENT

BY H. B. GUPPY.

"The island must have played the same rôle as regards the continent, whether in the Atlantic or in the Pacific, or in the Indian Ocean. If a group displays a certain relation in its floral features to a bordering continent in one ocean, other groups should display the same relation to the bordering mainland in the other oceans. There may be similarity in behaviour in these respects co-existent with great dissimilarity in floras. I don't suppose that there is any conspicuous peculiarity in the insular floras of Macaronesia, Lemuria, Malaya, Polynesia, and the Antilles that was not originally characteristic, though in a less specialised form, of one or other of the great land-masses. Islands appeal to me more as registers of past floral conditions in the continents than as representing their present state. Their marked peculiarities bear the impress of the past on the continents, whilst their common features tell the story of the present...." (The above is a quotation, with slight emendations, from a letter of mine to the Editor; and I am indebted to his courtesy for the opportunity of extending the thesis.)

THE most significant feature of insular floras is to be found in their peculiar and often "kinless" genera; and the mode of interpreting this feature largely determines our outlook on plant-development in islands. Either they are the highly specialised products of the islands, in which the ancestral characters excepting those of the family type have often largely disappeared, or they are the modified forms of allied continental genera that have in great part passed away. In the one case they would be the first of their race "destined, mayhap, to increase and become in future as common as they are now rare." In the second case they are the last of their race doomed to go the way of those countless forms of vegetable life that once peopled the globe and are now extinct.

It was with issues such as these that Hooker was mainly concerned in his lecture on Insular Floras delivered before the British Association at Nottingham in 1866. Although the potentialities and the probabilities involved in island-floras were treated in the lecture with a master's hand, we seem to be farther from the solution of the problem of these strange island-types in 1918 than Hooker was in 1866. We are still asking his question, Are they the first or the last of their race? Until that question is answered, and answered as Hooker answered it, we cannot hope to make any progress with insular floras; and if we cannot make any progress with the plant-history of the island we shall certainly be unable to do so with respect to the continent, where the same issues are raised but in a far more complex shape.

How, we may ask, did Hooker answer the question whether the peculiar insular types were the first or the last of their race? Islands were for him not only the last homes for the ancient races of mankind that had been driven from the continents through the pressure of superior races, but they were refuges for the ancient vegetation on the continents, or sanctuaries for the survivors of the successive revolutions of the plant-world on the mainland; in other words they were homes for the "relics of a far more ancient vegetation than now prevails on the mainland." He saw in the peculiar types of the Canarian and Madeiran woods the wrecks of a very ancient flora that flourished during the warmer and moister Tertiary period in the adjacent continental regions, but had since been expelled with the oncome of the age of aridity. In the peculiar American, African and Oriental types of the Macaronesian islands he saw witnesses of an age when the forests that encircled the warmer zones of the globe presented an association of plant-types now separated from each other by the breadths of continents and oceans, but still preserved in the Atlantic islands. And he extended his view to islands in general, regarding their assemblages of strange plant-types as gatherings of the clans of the plant-world that had fought their fight on the continents and had been expelled ages since.

But, as just implied, the matter does not end with Madeira and the Canary group. There are islands on the other side of Africa; and if Macaronesia displays its record of floral conditions that have passed away on the mainland, similar changes in the history of the plant-world ought to be registered in the islands, large and small, of the Mascarene region on the other side of the continent. If this is true of Africa we should expect the same of Asia and the New World. On all the islands that border them and lie between we should look for remnants of floral ages that have passed away on the continents. We should read in the stories of the arborescent *Compositae*, of the Tree-lobelias of Hawaii, and of the mysterious family of the *Sapotaceae*, of which the islands possess far more than their share, the tales of the continent. Even in the prevailing shrubby and arborescent habit of the strange genera of the islands, where endemic herbaceous plants rarely figure, we should expect to find an illustration of the original habit of growth of the plants in their continental homes.

The larger the island the more it will have to tell us of the continents, and as a rule the farther will its record go back. Australia, the great back-water of the evolutionary stream, will be the most communicative of all. We shall look to it to tell us of lost eras, not only on the Asiatic main but over much of the globe, eras affecting not merely its plants, but its animals, and its people. New Zealand in its features common to Australia will tell us of the present; but of the preceding ages, when Australia acquired most of its distinctive characters, it has often little to say. Yet it supplies indications of ages still more remote, and in this respect it stands first among the

islands. We shall look to Madagascar, another great backwater of the Old World, for its tale of lost ages in the tropical zone, not only of the eastern but of the western world, since there seems scarcely a case of discontinuous distribution affecting both worlds in which Madagascar or one of the lesser Mascarene islands does not figure. But its story will be tropical; and Distribution, as we are now realising, is primarily an affair of the tropics. The smaller Mascarene islands will in turn help us to unriddle the story of the later eras in the history of Lemuria; and their island-satellites will tell us of the latest of the lapsed ages; and so down the scale until we reach the coral island that will tell us only of the present. Then in the New World we shall look to the Antilles, large and small, each telling its story according to its size, to illuminate gone ages on the tropical mainland.

Yet under the strain of the test of comparison some insular regions will lose a portion of their interest. The Galapagos Islands with scarcely a genus of their own will have little to tell us beyond the last phase of the plant-world in tropical America; and very suggestive is it that a family like the *Amarantaceae*, which we are wont to associate with weeds in the tropical zone, should stand among the foremost in this group for its display of endemism. Were it not for its strange Cactus-forms the Galapagos Islands would tell us little of the plant-world in the past.

And as we began with the Macaronesian islands, so we will end with them. They seem to tell us more of the past than of the present. They teach us but little of the most recent age when Central Africa came under the dominion of Asiatic or rather Indian plants; but in their lowest African zone they tell us much of the long eras of aridity that have held most of the continent in bondage; and in their Laurel woods, some 1500 or 2000 feet up their slopes, they speak plainly of that earlier Mid-Tertiary period when moist climatic conditions prevailed in northern Africa. At that time the shores of the great inland Saharan sea were clothed, almost for the continent's breadth, with woods composed of plant-types that then girdled the globe, but now only survive in widely removed localities of the tropical and subtropical zones. As with the Atlantic islands, so with those of the other oceans there will ever be the story of the lagging of the insular floras.

The questions raised by Hooker as to previous continental connections and to means of oceanic transport ought now to be regarded as sufficiently answered. Yet we are still treating them as debatable issues. More than half a century has passed since 1866. Yet we are still speculating as to whether this or that group of islands was ever a part of a continent, and we are still discussing means of dispersal. In the interests of progress it would be best generally to regard such matters as dead not living issues, and to accept the situation that as exclusive factors in the stocking of oceanic islands the dispersing agencies begin where the range of Conifers ends. In the Pacific, for instance, we should rope in Fiji with all the large islands westward and

southward as originally continental. All the other large elevated Pacific groups, being non-coniferous in the sense of not holding truly indigenous representatives of the order, should be viewed as lying within the capacity of the dispersing agencies for their complete plant-stocking. The selection of the Conifers as our guide to past continental extensions will generally serve our purpose. Some evident exceptions of course exist, as in the cases of bird-dispersed genera like *Juniperus* and *Taxus* which occur in the North Atlantic islands. Even the disputed point concerned with islands and continental extensions should for practical purposes be viewed as in a general sense settled. Between those who consider that islands have always been islands and those who would regard all oceanic elevated islands as remnants of lost continents there is a middle position; and we can follow no safer lead in disputed areas than the guidance of the Conifers.

But Hooker in his lecture on insular floras treats of many themes, of which only a few are enlarged upon here. The setting of this lecture is worth recalling. It was delivered in a momentous period in the history of science. The outworks of the great citadel of the "special creationists" had been carried, not the citadel itself as was then imagined. But, outwork or citadel, the new creed gave the charter of liberty to the student of nature, and Hooker's lecture was in a general sense a justification of the Darwinian position. It matters little whether Darwin and his two great lieutenants, Hooker and Huxley, were always in agreement in their advocacy of the new faith. In fact they were radically divergent in some points. But it matters much that they broke the chains and set the inquirer free to pursue his investigations. Whether we have always used our freedom wisely is very doubtful. The tendency to drift aimlessly is not very re-assuring; and that is why with distribution, as with evolution, it is necessary to go back to beginnings and pick up the old lights we lost long ago.

STUDIES IN THE ECOLOGY OF TROPICAL RAIN-FOREST:

WITH SPECIAL REFERENCE TO THE FORESTS OF SOUTH BRAZIL

BY R. C. MCLEAN.

(With Plate I and twenty-one Figures in the Text.)

INTRODUCTION AND PART I. HUMIDITY.

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INTRODUCTION.

1. **Topography and Climate.** The region in which these observations were made is that of the rich forest on the slopes of the hills and in the valleys round about Rio de Janeiro, Southern Brazil. Rio de Janeiro is among the most lovely places in the world and has been many a time described, but

so far as I am aware never from the ecological standpoint. A few words of general introduction may not be out of place.

The coast of South America at this point runs due east and west, and the bay of Rio de Janeiro is an almost land-locked inlet, some forty miles long and of varying breadth. At the entrance it is only about a mile across, but farther inland it spreads out into a shallow expanse, nearly twenty miles in breadth, and dotted with numberless swampy islands. All around this gulf rise precipitous mountains, which form part of the extensive coast range, or Serra do Mar, of South Brazil.

The marshy shores of the bay are bordered by mangrove, except where the city of Rio and its suburbs lie, but the mountain slopes and the upper valleys are covered with dense rain-forest, only the sheerest and smoothest of the granite peaks being free from vegetation.

In spite of administrative laxity in the past the physical features of the forest lands have saved them from desecration at the hands of timber exploiters, inasmuch as it is next to impossible to transport logs on these steep slopes, so that they remain to-day in almost pristine grandeur over large areas, even near the city. At the present time forest patrols are responsible for guarding the Government's monopoly interest in what clearing may be possible. The conformation of these forest-clad hills is peculiar, and deserves description. Each consists of a granitic core, intruded originally into the gneiss, which has now been eroded from all around their upper portions. These granite masses have themselves weathered but slightly, and they stand up bare and sheer, like gigantic walls above the foliage on the lower slopes. The remaining gneiss forms rather steep slopes round the lower portions of the peaks, and as it weathers easily into soil, not an inch of it remains uncovered by forest.

Close to Rio itself the mountains vary between three and four thousand feet in height, but the forest-clad slopes rarely reach to more than half this height. On the other side of the bay, however, the lateral range known as the Organ Mountains attains a height of seven thousand feet, and there, the conditions of the mountain structure being different, the forest reaches almost to their full altitude.

Thus true rain-forest in this neighbourhood runs from the sea-level up to about fifteen hundred feet; though in the steep valleys between the peaks the forest naturally reaches a greater height than upon the skirts of the peaks themselves.

Above the level of true rain-forest there is often another type developed; an opener, dwarfer and much drier forest, which may be called "secondary-forest." Sometimes, as on Corcovado, rain-forest passes insensibly upwards into the secondary-forest, but more commonly the break between the two types is a decided one.

On the flat-topped mountain called the *Pedra da Gavea* (Pl. I) there is



The "Pedra da Gavea," west of Rio de Janeiro. Height about 1000 metres. The cone is granitic, capped by a metamorphic rock which forms a small plateau bearing a xerophytic woodland and a tussock association of grasses. The striped appearance is due to algae growing in the drainage channels. Taken from close to the sea-shore.

MCLEAN—BRAZILIAN RAIN-Forest (pp. 5—54).

a still more xerophytic type of forest, growing on the rocky summit plateau, and isolated from the lower vegetation by a great wall of almost inaccessible rock. This forest and an associated tussock grassland still await investigation.

The photograph is taken from close to the shore of the Atlantic and shows the basal slopes of gneiss, covered with dense rain-forest. Above this rises abruptly the smooth granite core, capped in this case by some hard metamorphic rock which forms a summit plateau. The surface of the granite mass is too smooth to allow foothold to large plants, and it is colonized on all these hills by extremely pronounced petrophytes, chiefly Orchidaceae, Cactaceae, Velloziaceae and some Bromeliaceae.

The larger part of the rock surface is covered by blue-green algae, which form great dark stripes upon it, following presumably the lines of water-drainage, and resembling the stripes of similar nature sometimes to be observed upon the sides of great buildings in Europe. These stripes are well shown in the photograph. It will be easily understood that the extent of rock surface available for close examination is decidedly limited. On the portions examined, however, I observed no mosses and few lichens and I imagine that the primary colonizers, preparing the meagre soil which supports at some points the typically xerophytic Angiosperms above-mentioned, are the Myxophyceae and a species of *Trentepohlia*¹ which is extremely abundant on the damper patches, lending, as Warming mentions, a characteristic tinge to the whole surface.

As the granite is only very slightly jointed, chasmophytes do not get much chance to colonize it².

Above the level of the true rain-forest a few patches of secondary-forest appear in the illustration. The ridge and shoulder to the right are crowned with this drier forest, which extends also a little way down the gully. On the left-hand side a few patches, completely isolated from the rain-forest below, may also be seen.

The summit-forest, which crowns the skyline, is still more xerophytic in character than the secondary-forest of the slopes, and is completely isolated from it.

As the Pedra da Gavea is backed by a deep valley running up from the sea, the climatic and rainfall conditions are very similar on both sides. The same is true of all the mountains in the vicinity of Rio. They are completely immersed in the moist coastal zone and are not lofty enough to differentiate much the climate on their opposite flanks.

The heights of the principal peaks are as follows: Tijuca, 3300 ft. (this is the highest point near Rio); Pedra da Gavea, 3000 ft. (*circa*); Corcovado, 2200 ft.

¹ *Trentepohlia aurea* (L.) Mart.

² The Angiosperm colonists would mostly fall into the category of Exochomophytes in Ötli's scheme (1903), see **Warming** (1909).

Their position in respect of Rio city itself is unique for mountains of such height. The main part of the city lies near the seaward opening of the bay, and is limited to the narrow edging of flat ground and low hills between the mountain of Corcovado and the several small indentations of the bay. This portion of the city ends with the suburb of Gavea, near the mountain of that name. The other half is much more extensive, and spreads out into suburbs which run for many miles along the northern skirts of the mountains. Rio is thus practically cut in two by the Corcovado group, and without doubt certain differences in climate are produced by this intervention.

The National Observatory, at which very full meteorological data are collected, lies in the city, to the north-west of Corcovado. On the other side, in a small valley leading up from the Lagoa Roderigo da Freitas and close to the Botanic Gardens, there is a government cultural experimental station, known as the "Horto Florestal." Here also meteorological records have been collected, which it is interesting to compare with the records from the other side of Corcovado. The following figures represent observations of climatic salients made at the Horto Florestal during 1912. These are extracted from tables provided by the Director of the above station.

Horto Florestal.

<i>Temperature</i>	Highest mean	February	26.2° C.
	Lowest mean	July	17.7° C.
<i>Relative Humidity</i>	Highest mean	May	86.1 %
	Lowest mean	December	71.5 %
<i>Rainfall</i>	Highest	July	550.5 mms.
	Lowest	December	67.7 mms.

It is striking to note that in spite of the very heavy July rainfall the absolute humidity for this month is almost the lowest for the year (12.6), the lowest being in September (12.5), with a heavy rainfall also (243.4 mms.).

The factor of nebulosity is arbitrarily reckoned on the basis of a scale from 0—10. In this reckoning 0 corresponds to a sky perfectly clear and 10 to a sky perfectly covered by clouds¹. From these observations averages of more or less accuracy may be extracted. At the Horto Florestal in 1912 the *highest* monthly mean was 7.4, for October and January, and the *lowest* 4.7, for June. As the variation for the above year corresponds exactly to the annual variation observed in Rio over a period of ten years, it may be regarded as the rule.

The climatic data for the city of Rio, recorded at the Observatory, are tabulated below, the salients selected being those which compare with the above figures from the Horto Florestal.

¹ *Boletim Mensal do Observatorio do Rio de Janeiro*, Jan., Feb., March, 1908, p. 15.

Rio Observatory.

<i>Temperature</i>	Highest mean	February	25.7° C.
	Lowest mean	July	19.19° C.
<i>Relative Humidity</i>	Highest mean	September	80.1 %
	Lowest mean	August	76.5 %
<i>Rainfall</i>	Highest	December	139.0 mms.
	Lowest	July	39.4 mms.
<i>Nebulosity</i>	Highest	October	7.3
	Lowest	July	4.9

These figures are averages for the period 1891–1905. For the preceding period 1871–1890 the temperatures are slightly higher, and the difference between the extremes of relative humidity rather less, but the variation is slight in all cases; while for the long period 1851–1890 the rainfall and temperature averages are almost exactly the same as those given above. A few features of difference between the two sides of the mountains are noticeable in comparing the records from these two points. Firstly, it is true the temperatures are very similar both in intensity and incidence, and when the interdependence of temperature and humidity is borne in mind this is striking; for the maximum and minimum relative humidities, although similar in degree, are very different in their incidence in time.

Secondly, the rainfall shows a great disparity. My own readings taken at the Botanic Gardens, close by the Horto, confirm the accuracy of the latter observations, and there can be small doubt that the rainfall at the Horto is greatly in excess of that on the Rio side of Corcovado.

The fact of the rainfall being, in the absolute, higher on the Horto side is indisputable, however it may be distributed¹. Apart from this excess of precipitation on the latter side the differences of climate are not important. On both sides of Corcovado the range of temperature is similar, on both sides the hot months are the wet months, and these months are marked by high relative and absolute humidities which are similar in both cases. As the variation in the rainfall is not too great to be compassed within the limits of a single type of climate, the coincidence of the humidity and temperature factors and the aforementioned nebulosity, render it evident that on both faces we are dealing with a climate essentially similar.

That this should be so is not after all very surprising, when the comparatively small elevation of the Corcovado range is considered. The prevailing wind on this coast is slightly east of south (*vide* "*O Clima de Rio de Janeiro*," 1892) and this, striking the abrupt rise of the mountains, naturally precipitates heavily upon their shoreward side, while passing with less disturbance over the foothills upon which stands the city itself. But, so far from the Corcovado group seriously diminishing the water supply on their leeward side, the ground there is largely swamp. The stream of moist air, upon which the character of the climate chiefly depends, is of too great a depth, apparently, to be wholly interrupted by so moderate an elevation as 3000 feet.

¹ The total precipitation at the Horto in 1912 was 2.238 metres.

An everyday observation supports this idea. The intensity of the sun's rays in Rio, even in the height of summer, with vertical illumination, is never extremely high, so that none of the precautions against sunstroke, which are inevitable in similar latitudes of the Old World tropics, seems to be necessary. Although under full insolation, neither animals nor herbage suffer as they do in the Indies or in Africa, an effect which is most probably, if not certainly, attributable to a great depth of very moist air, derived from the immense ocean spaces over which the dominant winds travel.

The intimate connection between Rio and the Corcovado group of mountains is strikingly unusual for a city of such size. The vertical walls of rock rise in some places literally from the streets, and animals from the jungle not infrequently enter the town. The site is so uneven and broken up by volcanic bosses that even in the centre of the city there rise here and there inaccessible knolls crowned with untouched forest.

It must not be supposed however that this plutonic *massif* forms an isolated group of peaks. It is simply a spur of the great Serra do Mar, which runs, roughly, from Sta. Catherina¹ along the coast to the north of Victoria in the State of Espiritu Santo, a distance of about 900 miles. The range is extended by lower hills northwards to the Rio S. Francisco, a further 750 miles. This great and irregular range delimits a coastal strip of hot moist country which all along is of the character typified by the portion near to Rio.

Passing inland across the watershed of this range the rainfall lessens, and a plateau is reached of rich arable land from which forest has been mostly removed. In many neighbourhoods the ground, cleared of forest by burning, has been allowed to degenerate into coarse grassland, covered by a rank growth of *Tristegis glutinosa*², a sweet tasting but very glutinous grass, which may reach three feet in height. This is of use only as grazing ground³. The drop in the rainfall is not considerable enough to render the growth of rain-forest impossible, and consequently all over this plateau the open country, cultivated or pastoral, is still variegated by patches of forest, often, for example, on hill tops where it has not been disturbed by clearing, rivalling the forest of the coastal zone in luxuriance, though poorer in species. Especially is this the case near the larger rivers, where forest and palm-brakes alternate with swamps in which beds of Marantaceae and Araceae produce a stately effect, suggestive indeed of horticulture and deliberate design.

The climate of this plateau is in all respects less tropical than that of the coast region. The further (inland) limit of this plateau is the Serra da Mantagueira, which is reputed the highest in Brazil, reaching 10,600 feet at the peak of Itatiaiaossu. This is sufficient to mark a decided break in the

¹ The classic ground of Fritz Müller's work.

² The "capimela" of the Brazilians.

³ A large scale demonstration of the folly of indiscriminate clearing in the tropics, originating in ignorance of the ecological conditions of the natural vegetation.

climate and beyond it we enter upon the "Campos" country, a strip of xerophytic steppe and savannah between the last-named range and the watershed of the Amazon tributaries, once across which we soon again enter forest country. Such in brief outline is the distribution of climate in South Brazil, by which the climatological status of our area round Rio may be judged.

Observations were carried out in the forest all round Rio, and to a less extent on the plateau on the inner side of the Serra do Mar. A visit was also paid to some extremely rich forests on the Serra do Mar farther to the south-west, near Santos.

The centre of operations was, however, at the Jardim Botânico of Rio, which lies on the south-west side of Corcovado, neighbouring the Horto Florestal. This is outside the true city area altogether. The gardens lie at the mouth of a short valley running up between Corcovado (which almost overhangs it) and a smaller hill. The gardens provide extremely good accommodation for research, and a complete equipment of material. Attached to the gardens is a small hill, some 200 feet in height, an outlier of the loftier neighbours of Corcovado behind it, and covered with forest of great luxuriance, true rain-forest, which is part of the general mountain-forest of the neighbourhood. As this area is included within the garden boundaries it has been protected from indiscriminate cutting. Some cutting has been done in the past, but the forest on this hill, although not among the richest portions in point of species, remains an adequately representative sample of all around it. It includes slopes in three directions, a flat piece upon the top, a small ravine and a stream of water, and an example of a rather rare phenomenon in tropical rain-forest, i.e. a pure society of a single species of palm¹.

The nature of this small hill, in view of its immediate proximity to the garden and the laboratories, marked it out as a suitable centre for experimental work, and it was accordingly so employed during my whole stay in Rio.

The outline map in Fig. 1 shows the topographical relations of the gardens and the hill in question. The garden boundaries are indicated by the dotted line, and show the portion of the hill included within them.

Climate. It is not necessary here to do more than sketch the salient features of the climate of Rio de Janeiro, as the details which bear upon the experimental work are referred to particularly under the appropriate sections.

Firstly in regard to *Temperature*.

Records of temperature are available from 1781–1788 and 1851–1905. The mean annual temperature for the period 1781–1905 was 22.83° C. For maxima and minima we have only figures available from 1891–1905. During this period of fifteen years the absolute maximum recorded was 38.0° C., and the absolute minimum recorded was 11.2° C. The mean of monthly maxima

¹ *Asterocaryum Airi* von Martius.

during fifteen years was $26.2^{\circ}\text{C}.$, while the mean of monthly minima was $19.5^{\circ}\text{C}.$

It will thus be seen that Rio enjoys a rather high average temperature without very marked variation either above or below the general mean. The absolute maximum is distinctly high, while the absolute minimum is sufficiently high to be indicative of a tropical climate. There is no record of frost even on the mountain tops.

This is worthy of remark, for Rio is nearly $23^{\circ}\text{S}.$ in latitude and thus only just inside the Tropic of Capricorn. That a place in this geographical

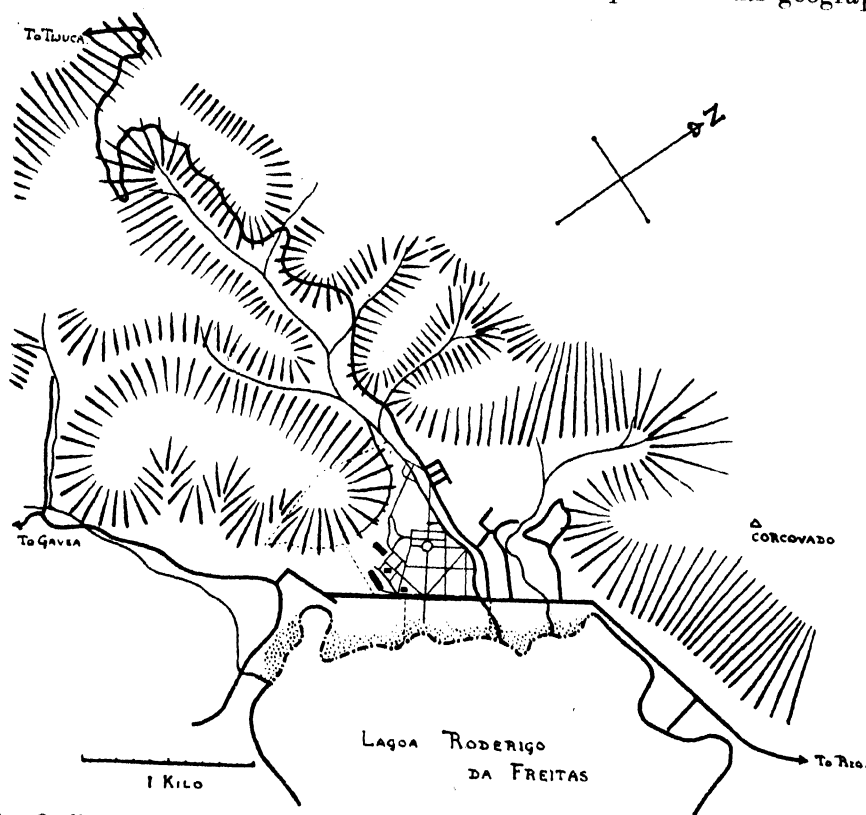


FIG. 1. Outline map of the Jardim Botânico and its environs. The gardens are in the middle, the paths shown by fine lines. To the left the fine dotted line marks the boundary of the forest area enclosed by the gardens, rising to about 200 ft. Below is the brackish "Lagoa" whose farther boundary is the Atlantic shore.

position should enjoy a climate which is thoroughly equatorial in character is attributable to the influence of the equatorial current which sweeps southward along this coast, extending the inter-tropical climate and vegetation a long way south of their actual geographical limit, almost in fact as far south as the Rio de la Plata, and well into Uruguay.

Next consider *Humidity*. For this records from 1891-1905 are also available.

The average for the entire period is 78·5 per cent. relative humidity—a fact which speaks for itself. The highest relative humidity recorded (in a fully open situation) was 84·5 per cent., and the lowest 69·7 per cent. Both these records, curiously enough, fall in the month of December, which according to the tables published is on the average a month of low humidity, though not so low as July, the month with minimal average.

This may be taken as indicative of an irregular distribution of humidity through the year.

In regard to absolute humidity we possess records of vapour tension for the same period as above, the general mean being 16·5. The absolute humidity depends upon evaporation, and that upon rainfall, which is a rigidly periodic function. Correspondingly the absolute humidity shows a periodic variation, being *highest* in the *hot* months (December—March). The curve follows very approximately that of rainfall. In correlation with the fact that the highest absolute humidity occurs in the hot months, the relative humidity then rises to a secondary maximum also, so that the period of the year when unfavourable conditions in regard to water supply are extreme is not that of the hot season, but rather during the colder months (May—September) when rainfall and humidity are at their lowest, and nebulosity also at its minimum. It may be pointed out that there is a remarkable similarity between the curves of relative humidity and nebulosity, illustrating the inter-relationship of the two factors.

Lastly about *Rainfall*.

The mean annual rainfall from 1851–1905 is 1·112 metres or 43·7 inches. This is surprisingly little when we put the elevated temperatures into relation with the high relative humidities, and suggests that the latter must depend largely on nebulosity rather than actual rain, which we have seen above to be probably the case.

Although the averages taken over long periods show a regular periodicity through the year, the cool months being also regularly dry and the hot months wet, yet the rainfall in particular months is apt to show large, anomalous departures from the usual averages. The annual rainfall remains, in spite of these irregularities, fairly constant about the figure given above, but the departures from the normal in several cases are enough to upset the periodic curve for that year entirely.

The climatic conditions of our region may be summed up in a few words: a high average temperature, the hottest period being from October to March and the coolest from April to September: a high average humidity, rising often to very high¹: a rainfall which is not strikingly high, but which is usually highest during the hot months and slight during the cold months: nebulosity, also high in the hot season, but showing a marked diminution

¹ Even in the absence of precipitation. The typical S.S.E. wind comes over an enormous tract of ocean.

during the cold months. This is perhaps the briefest outline which gives a clear conception of the facts.

I wish at this place to call attention to a method of analysis of climatic periodicity which might yield good results if applied to the solution of questions of plant distribution.

Schimper has drawn attention to the sensitiveness of plants to apparently slight environmental differences. Any method therefore which might aid in the investigation and particularly in the comparative valuation of climatic influences is likely to shed light upon periodic phenomena as a whole and possibly also on the balance of climatic and edaphic influences on distribution, and on questions of the relationships existing between plants and the soil constituents; for it has been suggested that cases in which the same species shows a varying relationship, whether of affinity or repulsion, to certain soil constituents, are susceptible of explanation on climatic grounds which either affect the plant's capacity for competition with allied species or affect its relation to the soil solution.

The method of analysis which I here put forward may not be new, but I am unaware that it has ever been applied to plant ecology, although the idea may be a familiar one, for aught I know, to pure climatologists. I believe it capable of bringing out in a clear and concise manner slight differences of climate.

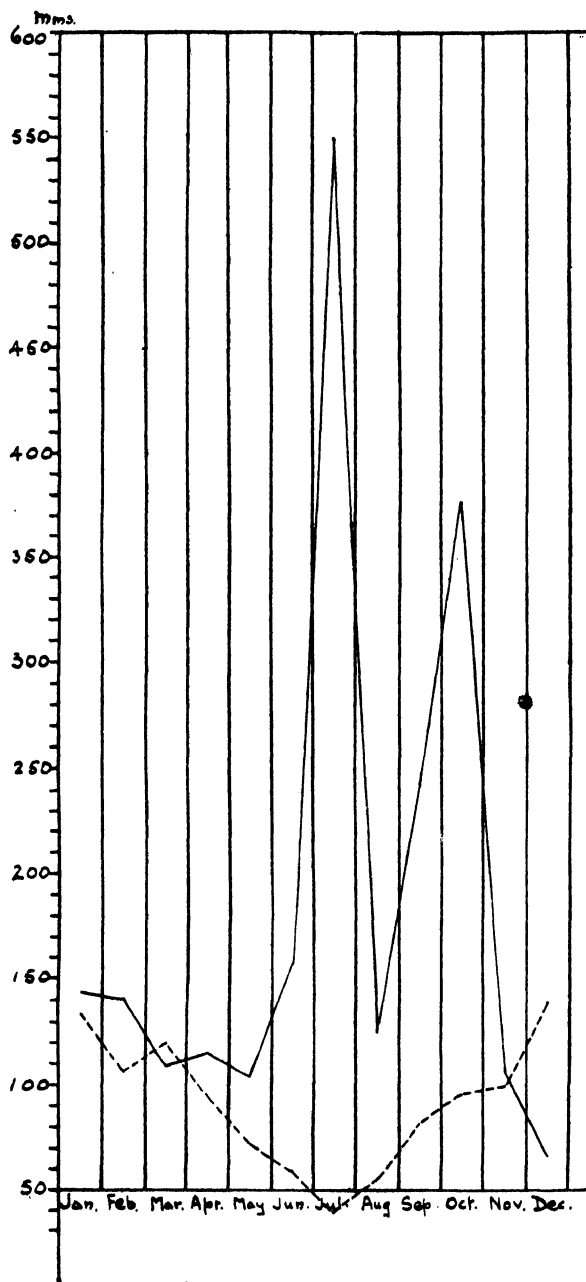


FIG. 2. Comparison of the Rainfall Records on both sides of Corcovado. Rainfall at Jardim Botânico during 1912 (continuous line) compared with the average rainfall of Rio for the years 1891-1905 (incl.) (dotted line).

It is possible to combine into a single graph the records of various factors, although expressed in diverse units, by the following simple means. Each month is divided into three decades, giving thirty-six approximately equal sections of the year. Then for each decade, and taking each factor separately in turn, we find the ratio subsisting between the actual record of the factor for that decade and the mean of the same factor for the year.

These ratios (between each climatic factor and its mean) are added together for each decade separately and the totals each divided by the number of factors employed. The 36 arithmetic means are then plotted to form a simple curve.

The factors concerned must be treated in such a way that for each one, considered singly, a rise would imply an increase in favourability in the climate, *ceteris paribus*.

Thus for the curve here reproduced the four factors used were temperature, relative humidity, rainfall, and clear days. The last represents the amount of sunshine received, perhaps even more effectively than simple sunshine records. Direct black-bulb records of solar radiation are not suitable for the purpose, as an increase in this is not necessarily favourable. The curve of nebulosity is exactly the reverse of the curve we wish to plot, but the curve representing the number of clear days (taken as being days in which nebulosity does not reach .5) is almost exactly the reciprocal of that of nebulosity and thus is suitable for our purpose.

Increase of each of these factors may be justly regarded as being favourable to vegetation, and *vice versa*, if other factors remain constant. Thus the final curve of their ratios with their means in each decade of the year will indicate the *general* favourability or otherwise of the climate, enabling comparisons of *total favourability* to be made. It must be admitted that this should not be regarded as perfectly attained in the present instance, for the number of factors concerned is limited to those whose effects upon plants

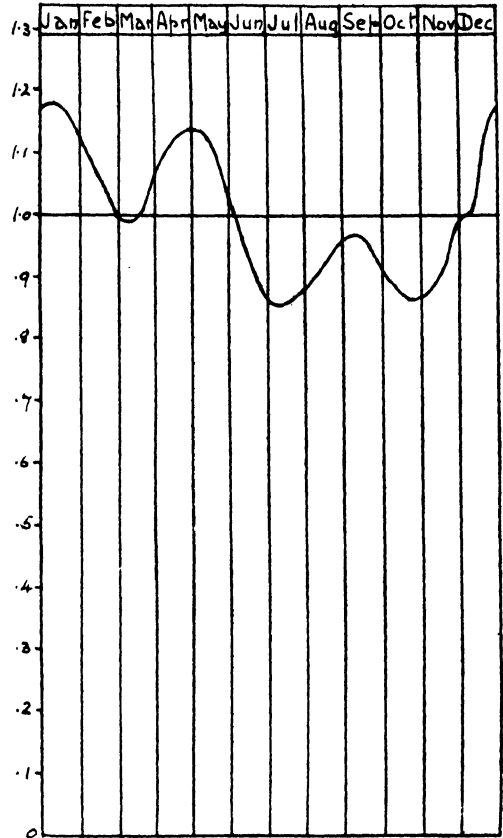


FIG. 3. Variation-cycle of Climatic Favourability as defined by the four factors: Temperature, Rainfall, Relative Humidity, and Sunshine. For explanation see text.

are tolerably well known; but it seems capable of further elaboration and expansion¹.

As far as this goes it may be remarked that there appears to be a decided periodicity for the year as a whole. The depressed temperature and rainfall for the months July to October lower the total favourability, in spite of a marked increase in sunshine, or rather "clear days."

Another point brought out is the declining favourability in February, which is usually regarded as the height of the hot and rainy season. This is due to the great nebulosity of the month. It will be noticed that there is a great rise in favourability at the end of the year, from practically the nadir at the end of October to the zenith in the beginning of January. By good fortune this coincides with the period of my visit, so that the experimental records, although over such a short period, really cover almost the extreme range of the climate. This rise in the curve also coincides, it is especially to be noticed, with the beginning of the growing and principal flowering season.

The climate may be said to be at its "norm," where the curve cuts the line of unity (where the average of the ratios is 1), in March, the first decade of June, and the first decade of December.

2. Objects and Methods. The objects in view were four: primarily the estimation, with what exactitude might be possible, of some of the ecological factors included under the titles of (1) Humidity and (2) Illumination.

Much has been written about the great humidity and dim light of tropical forests, but little or nothing has ever been done towards establishing an experimental estimate of what these things mean to the plants. The comparisons which have previously been made between tropical and temperate climates have dealt only with the open, and, except for a few isolated observations of Haberlandt's², I have sought in vain for any records made actually inside rain-forest, and was therefore obliged to begin from first principles.

It was also hoped to discover how these conditions affected the undergrowth plants, morphologically and otherwise, in relation to (3) the Transpiration Problem and (4) the Assimilation Problem.

No intensive study of a particular factor was attempted, but the idea followed was to sample the conditions as widely as possible in the very restricted time, merely to indicate the range and variety of the questions awaiting thorough and painstaking investigation, and obtain some rough idea of the incidence of the chief factors.

The methods employed could not be arranged beforehand, but were those which the conditions suggested and circumstances permitted at the time³.

¹ Since writing the above I find that a similar method has been employed by some human physiologists, though for a totally different purpose.

² Haberlandt, 1898.

³ A regular meteorological station was equipped at the Jardim Botânico at the end of 1913. Full details of its first year's observations are given in the *Archivos do Jardim Botânico*, 1, fasc. i, 1915.

3. Acknowledgments. My visit to Rio was due to an invitation from Dr J. C. Willis, the late Director of the Jardim Botânico, whose guest I was during my stay and who placed the resources of the Gardens freely at my service.

My gratitude is due to him and to all who assisted me in my investigations, particularly Senhores Dr Kopal and Dr Graciano, chiefs of the two laboratories in the Gardens; and Dr Armando Frazao, whose great kindness and help during my whole stay have placed me under the deepest obligation to him.

The work was completed at the Botany School, Cambridge.

PART I. HUMIDITY.

SECTION A. ATMOSPHERIC HUMIDITY.

(a) RECORDS OF ATMOSPHERIC CONDITIONS.

1. Humidity Records. As I have already mentioned, the general humidity of the air, even in the town, distant from all forest, is uniformly high. In Fig. 4 is reproduced a continuous hygrograph record which gives

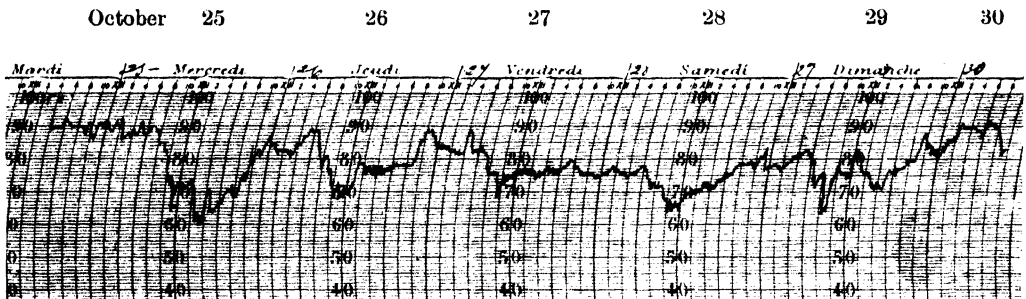


FIG. 4. Diurnal humidity at Rio Observatory from Oct. 24th–30th, 1912. The tracing shows a marked drop at or about midday, with a subsequent rise. On the 29th increasing nebulosity caused a reversal, with a secondary maximum at noon.

a more detailed idea of the diurnal variation of this factor in the open air, away from any vegetation. This record was taken at the Observatory while testing instruments which I afterwards used in taking records in the forest. This graph is therefore strictly comparable with those of the forest humidity given later on, having been made with the same instruments.

I must here express my great indebtedness to the Director of the National Observatory for the very kind loan of valuable recording instruments and also of standard thermometers and two rain-gauges, all of which were of the greatest possible assistance to me.

The diurnal variation deduced from the averages of fifteen years is a single curve with its maximum (81 per cent.) at 5 a.m. and its minimum

(73 per cent.) at 2 p.m. This is a simple variation caused almost certainly by insolation. The above graph shows, however, almost the reverse variation on several occasions, the maximum lying near midday. This may I believe be accounted for by a spell of increased nebulosity. Under a vertical sun the intervention of a cloud layer of moderate intensity scarcely suffices at all to reduce the temperature, but the drop under heavy clouding is marked, and is of course reflected in higher relative humidity.

Turning from these records, I include firstly a specimen record made in the laboratory close to my forest area. There the humidity is consistently higher and the variation smaller, although the laboratory stands clear of vegetation.

In the forest a large tree of *Piptadenia communis* which possessed a straight trunk rising from an undergrowth of average density was chosen as

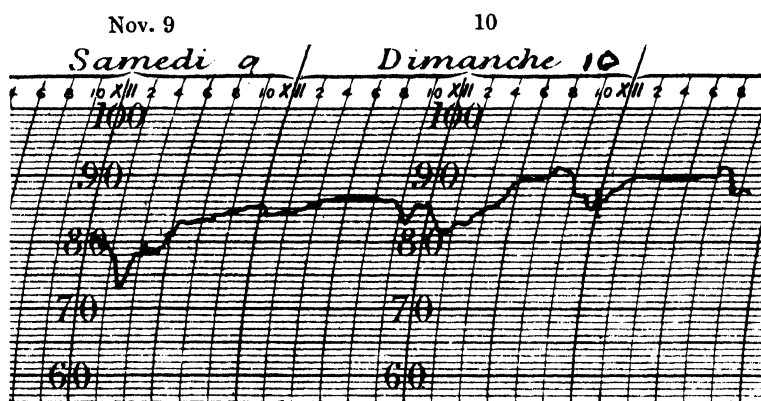


FIG. 5. Humidity in the Laboratory, Jardim Botânico. A curve of the same typical form as in Fig. 4, but with less irregularity and a smaller amplitude.

a base-station for all experimental work. This was near the base of the forest-covered hill, and stood about 150-200 yards from the nearest edge of the jungle. To this tree were affixed two little instrument shelters with sloping roofs, open in front and with the sides also pierced with large holes to allow free circulation of air. One of these was fixed at a height of *one metre* and formed the "low-level station" while the other stood at a height of *four metres*, clear of the undergrowth, and formed the "high-level station."

These shelters were some two feet square, and served only to protect the instruments from drips—all that was needful owing to the thick canopy of foliage overhead—but instruments in them were otherwise exposed to every variation of conditions, including the access of sun-rays, a matter of note.

In Fig. 6 is a continuous graph of the humidities at the low-level—that is, one metre above the soil and among the bushes of the undergrowth¹.

¹ In order to mark the way to any chosen spot in a tropical forest it is essential to blaze the track in some way. Red tags tied on the bushes are effective.

The continuance of an unvaried humidity of 95 per cent. from 6 p.m. on Friday till 10 a.m. on Sunday is particularly striking, but it is paralleled by similar although shorter spells of unchanged humidity at other points in the record. This I believe is a fact which has not before been demonstrated, and

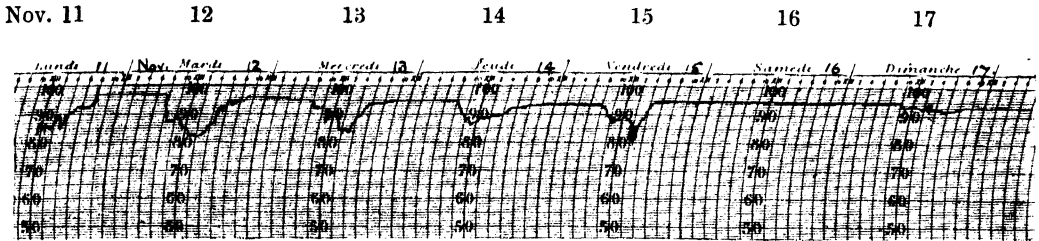


FIG. 6. Humidity at low-level in forest, from Nov. 11th—17th, 1912. Note the high range of the curve, the small but regular midday fall, and the long periods of stagnancy.

the existence of such stretches of absolutely uniform humidity testifies to the density of the shelter and stagnancy of atmosphere produced by the undergrowth.

The periodical descent of the curve is to be accounted for in this way. The face of my hill lay towards E.S.E., but from due east it was shadowed by Corcovado. The sun, following a course to the northward, never shone vertically upon the hill-face, but when it overtopped Corcovado at seven a.m. or thereabouts, an immediate descent of the relative humidity is noticeable, and from then till six p.m. the humidity drops to between 70 and 80 per cent., rising again to a constant level at sunset. The minute variations in the mid-day curve are caused by the sun-rays or sun-flecks passing over the instrument.

An examination of the foregoing particulars serves to illustrate this fact: that sunshine causes a drop in the humidity, even in the lowest layers of the forest, of 15-20 per cent. and that sun-rays penetrating the foliage may cause a local lowering of the humidity to 60 per cent. or less, while at night or in sunless weather the humidity may stand unvaryingly at 95 per cent. or may even touch saturation point.

The next pair of graphs (Fig. 7) represent humidities recorded from the high-level, i.e. four metres above ground. This is above the level of all but the highest shrubs and so is in much opener air than the low-level station. Accordingly, the humidities show much greater variability than the former ones, and this variation is moreover more regular and consistent than at the lower level. Nevertheless it will be noticed that during the night the humidity rises as high as at the other level, that is to 95 per cent. and over, where it remains for several hours. During the sunny hours of the day the level falls much lower, comparatively, and the tiny fluctuations which in the case of the lower level records are attributed to sun-flecks passing over the instrument, are here, as one might expect, more numerous and more pronounced, because

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the instrument is shaded only by the lofty canopy of the high forest, not by shrubs near at hand.

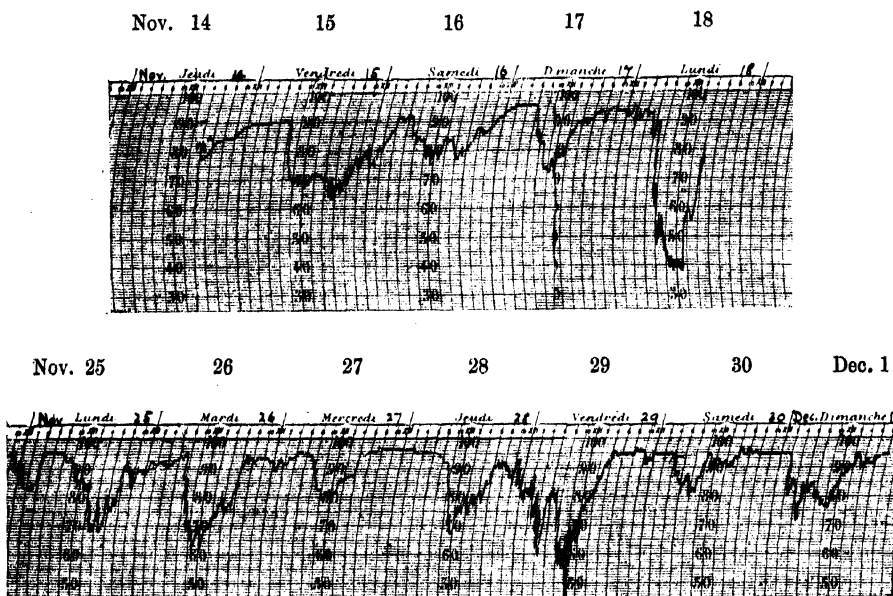


FIG. 7. Humidity at high-level in forest, from Nov. 14th—18th and from Nov. 25th—Dec. 1st, 1912. Note the much greater amplitude than in Fig. 6, the very marked midday fall, the incessant variation during daylight and the short periods of stagnancy at high ranges during the night. Compare the curves for Nov. 14th—17th as shown in the two Figs. 6 and 7.

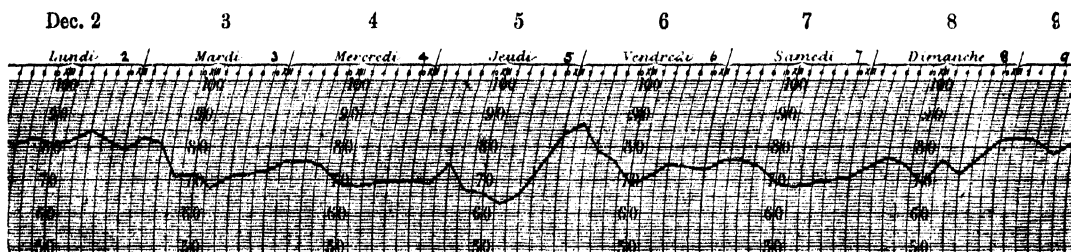


FIG. 8. Humidity in Rio City from Dec. 2nd—9th, 1912. Drawn from published observations. The range is considerably lower than in the forest (Figs. 6 and 7) and the amplitude less.

It is often assumed that the high-forest trees have to endure rather low humidities during the hottest hours of the day, but in South Brazil the ordinary open-air humidities are on the average so high that there cannot be anything very exacting for the trees to endure. In Fig. 8 is given a graph drawn from the published observations made at the Rio Observatory during this period. It will be seen by comparison that the records at the high-level in the forest itself resemble these Observatory records in essentials, sometimes showing an even lower range. This aberration is probably accounted for by the action of wind. The "Rosa Anemoscopica" published by the Observatory shows that wind from the S.S.E. prevails enormously over all

other directions. The face of my hill lay E.S.E., exposed fully to the wind, whereas the instruments on the terrace of the Observatory are not so exposed.

Apart from this, the average of relative humidity at the Observatory is lower than at the Botanic Gardens, as shown by the Horto Florestal records, so that it seems clear that even the highest stratum of trees—the “roof” of the forest as it were—is not exposed in ordinary circumstances to humidities as low as those which trees in our own climate are called upon to encounter.

In one peculiar way the forest protects itself in an automatic manner from the effects of strong solar radiation. The establishment of high relative humidities combined with high sun temperatures necessarily implies high rates of evaporation. The total amount of vapour transpired by the upper layers of the forest is doubtless very considerable, especially so in the case of forest growing on the higher and more exposed slopes of the mountains, and this vapour, rising along the precipitous mountain sides, condenses into clouds at a height of from 2000–3000 feet, shading the forest from which it has risen. Such “transpiration clouds” may be seen constantly overshadowing the forests in clear summer weather, even when the sky is elsewhere cloudless. I do not doubt that these clouds increase the nebulosity records for Rio to a considerable extent above those of inland stations of similar latitude, such as Sao Paulo, where the forests have been mostly cleared away.

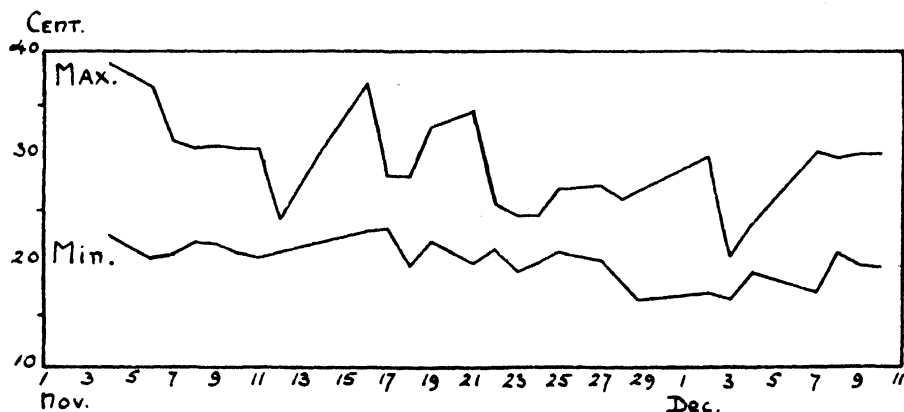


FIG. 9. Maximum and Minimum Temperatures in shade on the floor of the forest.
The two limits vary independently to a remarkable extent.

2. Temperature Records. The temperatures in the open have been dealt with previously, but readings were taken also in the deepest shade of the forest at the Base Station. A maximum and a minimum thermometer, lent and verified by the Observatory, were placed across twigs at about six inches above the soil level, shaded from the direct access of any sun-fleck by the bole of a large tree, and read every morning at ten o'clock, whenever possible, from November 4th to December 10th.

The readings are given in Fig. 9 and form an interesting contrast with the figures for the solar radiation published by the Observatory (*v. Pt. II*).

The temperatures in the forest are decidedly high for shade temperatures but it will be remarked that there is no close correspondence between the rise and fall of the two sets of records. Wind and evaporation are no doubt contributory causes introducing disturbance into the readings taken close to the forest floor.

As the internal temperatures in the jungle affect the vegetation, both indirectly by raising the amount of moisture which the air is capable of absorbing, and directly by the stimulus to metabolism and to decay and nitrification in the soil, I here lay some stress upon them. Their effect will be considered later.

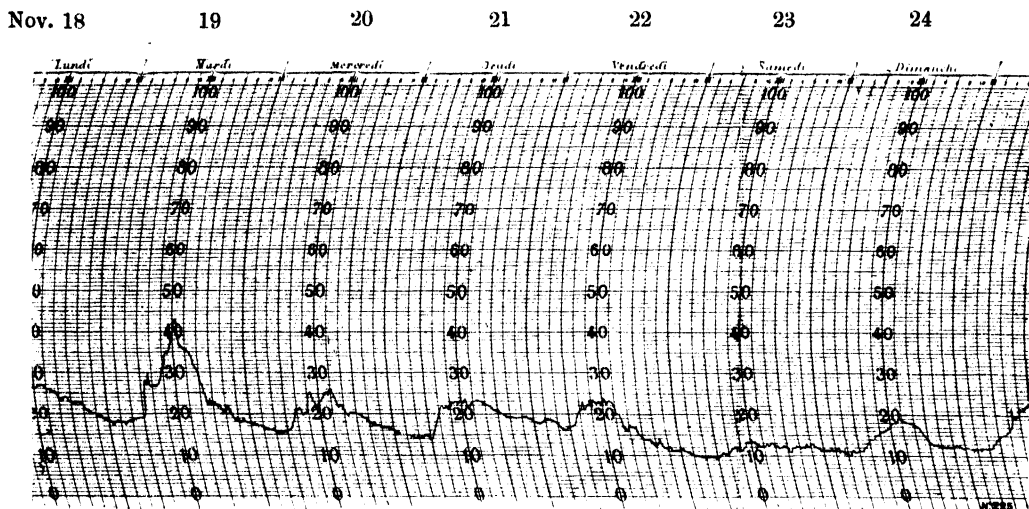


FIG. 10. Temperatures in the shade outside the forest, taken in the garden laboratory, Nov. 18th—24th, 1912, to be compared with Fig. 11. The high midday range on clear days is noteworthy, and the depression of the amplitude by nebulosity, as on Nov. 23rd. The very steep rise immediately after sunrise, about 6 a.m., is conspicuous.

Above is reproduced a continuous thermograph of the temperatures at the high-level box at my base station (four metres). The character of the curve corresponds very well with the record of shade-temperature *outside* the forest in the laboratory (Fig. 11), but shows a restricted range. As one might expect, the internal temperature of the forest maintains a higher average than the external world, but with a smaller fluctuation. Nevertheless, above the terrestrial shrub layer which cuts off the “upper levels” of the forest from the “ground levels” the readings of temperature as well as the humidity follow the fluctuations observed outside, induced by cloudiness, variation of humidity, etc., whereas the “ground levels” do not.

For comparison with the maximum and minimum records there is shown here (Fig. 12) a record of the temperatures taken in the lower-level box (one metre) with a delicate thermograph. This record, being less exposed to the effects of radiation and evaporation, probably gives a truer rendering of the air

temperatures. The remarkable constancy is at once evident. The average is low, about 21° C., but to compensate for that the drop in the early hours of the morning is much less appreciable than in the "upper levels."

The minima in the graph compare closely with the minima near the soil but the *maxima* are lower owing to the aforesaid causes.

3. Conclusions. The dense layer of terrestrial shrubs seems to cleave the forest into two portions, the lower possessing a climate cooler and more humid than the brighter regions above, less exposed to variation, and

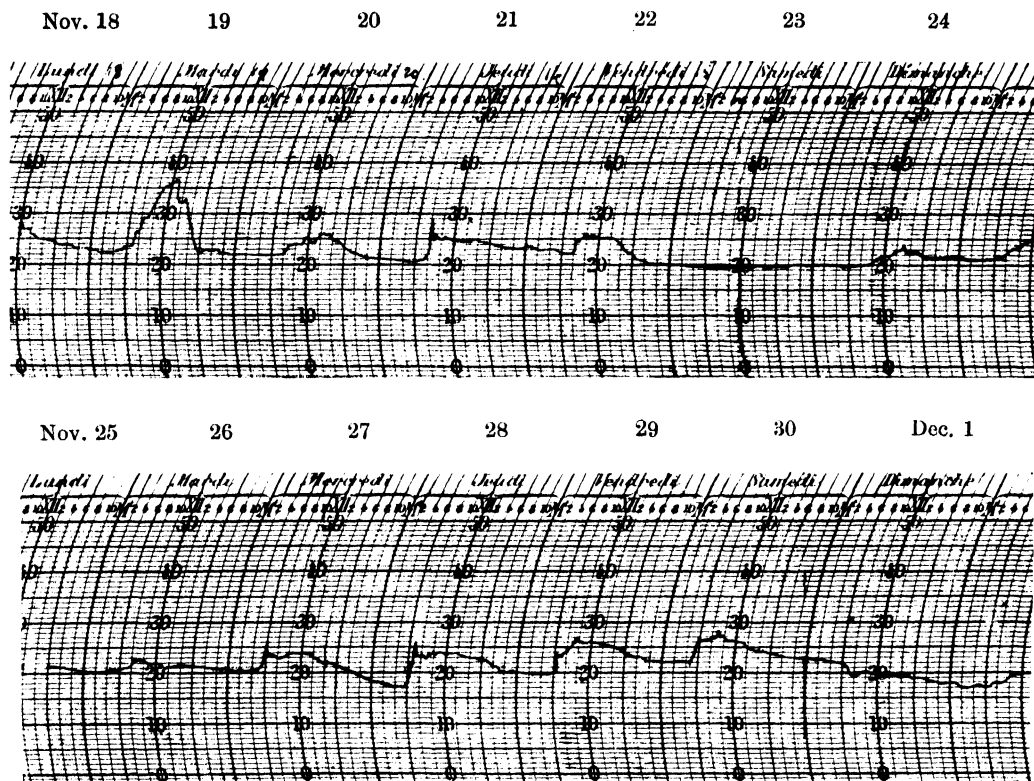


FIG. 11. High-level temperatures in forest. Nov. 18th—24th, and Nov. 25th—Dec. 1st, 1912.

It will be noticed that the upper curve shows, day for day, an obvious correspondence with the shade temperatures in the laboratory, but with a higher range and smaller amplitude. The sudden rise at sunrise is even more marked than externally in the open, as shown by Fig. 10.

less affected by conditions external to the forest. This is opposed to the generally accepted view that tropical rain-forests exhibit no phenomena of layering comparable with that in temperate forests. Above the terrestrial shrubs, the smaller trees and the epiphytes flourish under mesophytic conditions of atmosphere. Below the shrubs we find a world of small shrubs and herbs with whose peculiar environment I am now concerned. Both they and the shrubs are affected by the climate and the soil-conditions in an unfavour-

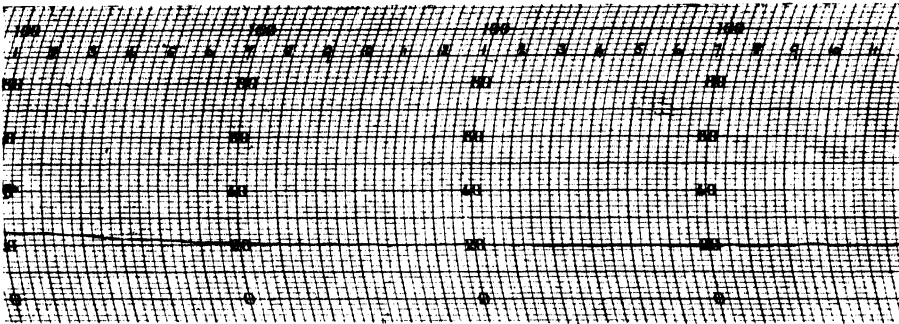
able manner. The higher layers, excepting the epiphytes, are of course subject to the same soil conditions, but their climate is temperate and favourable.

The high forest trees on the other hand, under the same soil conditions, have to face a climate almost the reverse of that experienced by the lower layers. The lowest and the highest layers present peculiar problems, and the experimental work here described touches only the lowest layers, where the conditions seem to be most unfavourable to vegetation.

Noon 22nd

Midnight

Noon 23rd



Noon 25th

Midnight

Noon 26th

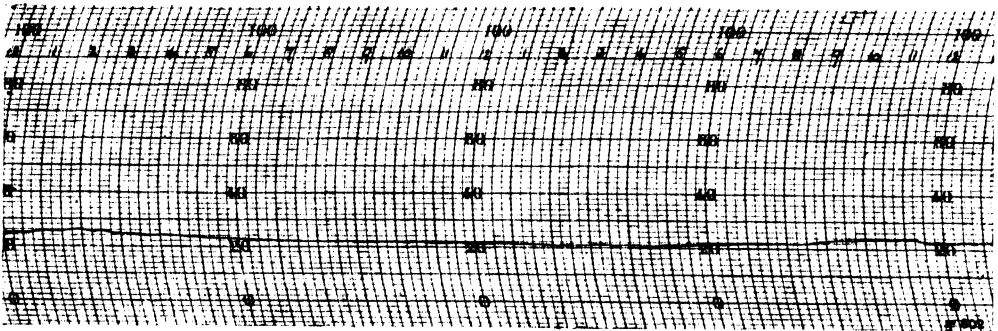


FIG. 12. Diurnal temperature curve taken in the low-level shelter in forest. Noon Nov. 22nd—noon Nov. 23rd, and noon Nov. 25th—noon Nov. 26th. The range is high and steady ($20^{\circ}\text{C}.$), even during the period of the early morning minimum shown in Figs. 10 and 11, and the amplitude is very small compared with the external temperatures.

(b) TRANSPIRATION EXPERIMENTS.

1. **Transpiration of Leaves of Different Types.** An estimate of the actual rate of transpiration going on in the lowest stratum of the forest was made by means of leaves severed under water and placed with their stalks in tubes of water, the surface being protected by a thin film of olive oil. These tubes were hung on a wire, between two plants, at a distance of only a few inches above the soil, and in the shade of shrubs. As a check of the atmospheric conditions, hygograph and thermograph records were taken

over the same period, the instruments being placed actually on the ground, while evaporation was measured by the loss in weight of a beaker of distilled water kept filled to within 3 mms. of the rim. The experiment extended from

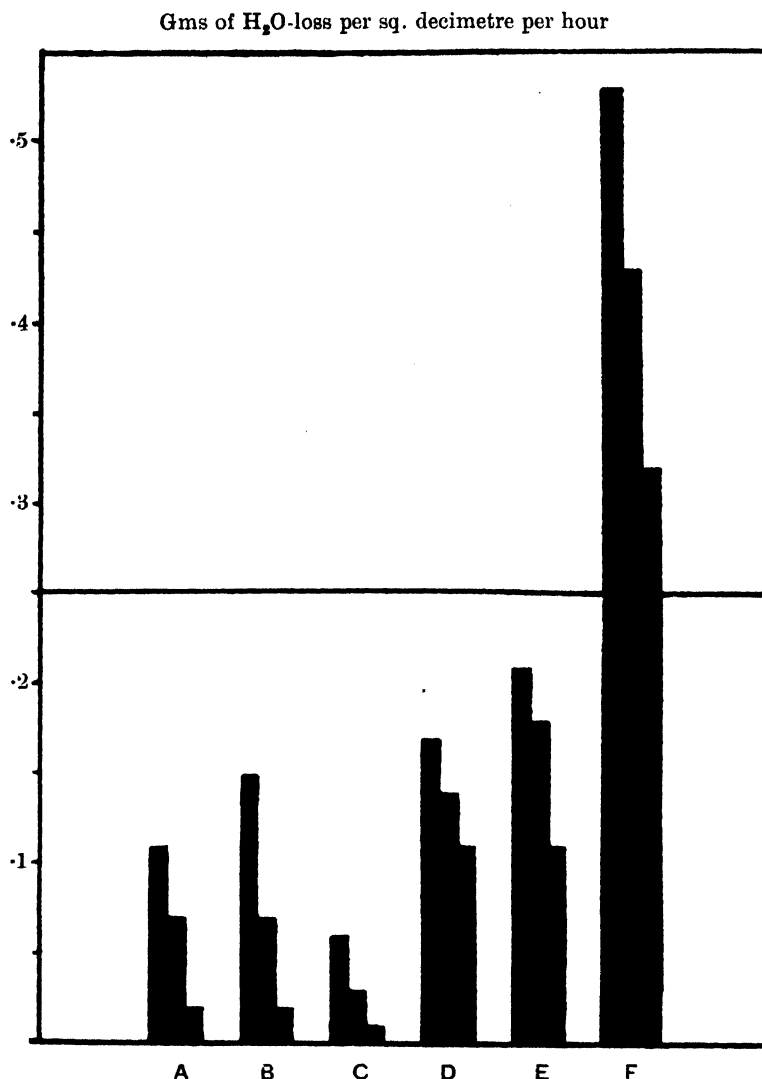


FIG. 13. Transpiration Test in Forest Undergrowth.

- | | |
|------------------------------|---------------------------------------|
| A. <i>Passiflora</i> sp. | B. <i>Acalypha communis</i> . |
| C. <i>Anthurium</i> sp. | D. <i>Mimosa sepiaria</i> . |
| E. <i>Echites peltatus</i> . | F. Free-surface evaporation of water. |

Each species is represented by three columns, which stand for the average transpiration over the periods (1) Dec. 9th—10th, (2) 10th—11th, (3) 11th—13th respectively.

December 9th to December 13th. Its further continuance was prevented by heavy rain.

I should like to emphasise the difficulties, both climatic and zoological, under which experimental work has to be carried out in the rain-forest.

Sudden changes of weather spoilt two previous attempts at the above enquiry, and at this third attempt one leaf was eaten by leaf-cutting ants, while personal difficulties are no slight trouble.

Free-surface evaporation appeared the only practicable method of measuring that factor, as both the porcelain pot atmometers set up at the forest base station became smothered in fungal hyphae in less than forty-eight hours.

In order that comparative data might be obtained, leaves of different biological types were chosen, both from the lower layers of the forest and from the open sunlight.

The following were used (Fig. 13):

Shade leaves of the forest:

<i>Anthurium</i> sp.	Deep green and glabrous, subcoriaceous
<i>Echites peltatus</i>	Surface velvety, texture herbaceous
<i>Mimosa sepiaria</i>	A tall shrub, leaves nyctitropic, compound bipinnate.

Sun leaves from the open garden:

<i>Acalypha communis</i>	Red, smooth surface, herbaceous
<i>Passiflora</i> sp.	Green, herbaceous, surface glabrous.

The areas were estimated afterwards by weighing paper replicas of the leaves and the average water loss in grams per square centimetre per hour are given below:

A. <i>Anthurium</i>	·00032 gm. per sq. cm. per hr. = 3·2 gms. per sq. met.
B. <i>Echites</i>	·0017 " " = 17·0 "
C. <i>Mimosa</i>	·0014 " " = 14·0 "
D. <i>Acalypha</i>	·00117 " " = 11·7 "
E. <i>Passiflora</i>	·00068 " " = 6·8 "

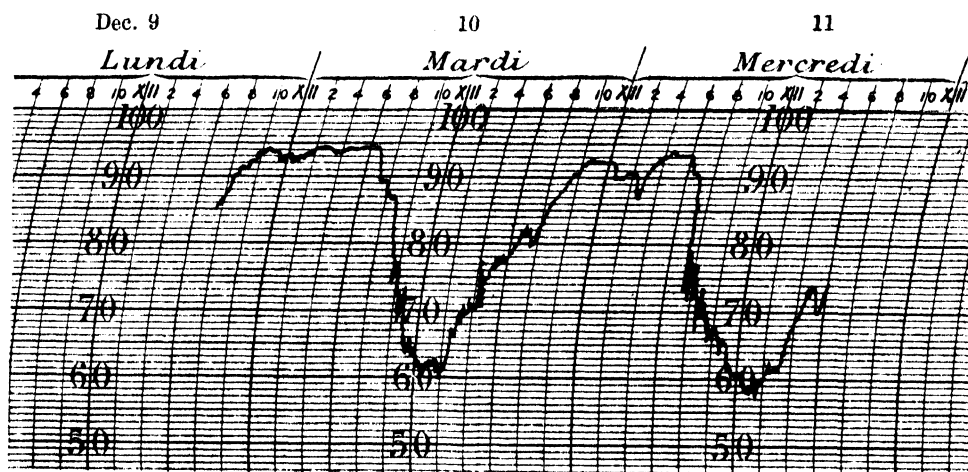


FIG. 14. Relative humidity on ground level during transpiration experiment.

The average evaporation over the same period, in the same units, was ·0043 gm. Thus it will be seen that the highest rate of water-loss found was only ·4 of the free aqueous evaporation. I append graphs illustrative of the conditions under which transpiration was carried on. The hygrograph (Fig. 14)

shows regular fluctuation between 60 and 95 per cent. The thermograph shows that the temperature only changed in a negligible degree over the period covered.

It will be noticed on referring to Fig. 13 that the evaporation of the water fell off considerably towards the end of the time, with a corresponding drop in the transpiration. This is quite independent of prevalent conditions exterior to the forest during the same period, as will be seen by reference to the graph of evaporation at Rio Observatory (Fig. 15). The comparatively slight effect of external meteorological conditions on these ground layers, as compared with the upper layers of the forest, is again emphasised by a comparison of the temperature chart (Fig. 14A) with the radiation intensities in the open for the same days, which average 46°C .

The imperfection of these investigations I regretfully acknowledge, and I give them solely because they are the first attempt of any sort to deal ecologically with this subject.

2. Comparison of the Types: Nyctitropism.

Comparison of the behaviour of the different types is interesting. In view of the difficulties of transpiration it is worth notice that the highest rate was shown by a typical undergrowth plant (*Echites*), possessed of the velvety leaf-surface which Schimper and others have remarked as common in like situations.

The nyctitropic folding of the leaves in mimosa did not seem to have any marked effect in lessening its water loss. This nyctitropic folding is remarkably prevalent in the forests of tropical America and no reason has I believe been yet proved satisfactory to account for it. I do not hesitate to say that it has at least no significance as a protection against water-loss, since the humidity appears in my records to be highest at night, and the leaves seem to lose water at a very moderate rate even during the hotter periods of the day. Further, more than 25 per cent. of the *undergrowth* plants possess pulvini to their leaves and show similar movements, although they are remote from any danger of excessive water-loss. The movement, it may be pointed out, is as often as not upwards and not downwards, thus increasing the exposure of the lower leaf-surfaces and the stomata. Nor does the structure of the

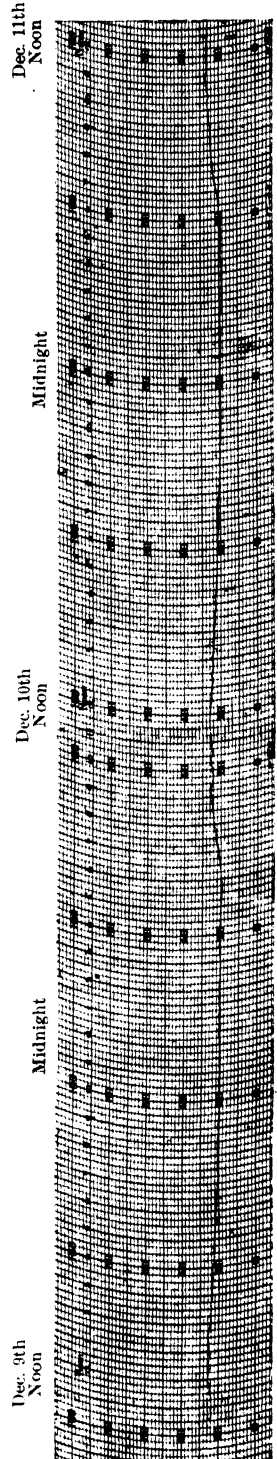


FIG. 14A. Temperatures during transpiration experiment.

pulvini throw any light on the question. In one of the commonest pulvinate species of the ground flora (*Calathea longifolia*) the section of the pulvinus is oval, with its longest diameter vertical. There is a zone of sclerenchyma completely encircling the lower portion of the pulvinus, but running in a horseshoe form round the lower sides only in the region where bending takes place, the upper surface being here occupied by a broad zone of collenchyma. This is probably a mechanical arrangement to facilitate bending¹. The cells of the ground tissue are large but firm-walled, with no noticeable intercellular pits for communication, and very small intercellular spaces. The bulk of this tissue is certainly passive. Excentrically, and nearer the upper surface, there is a core of much larger

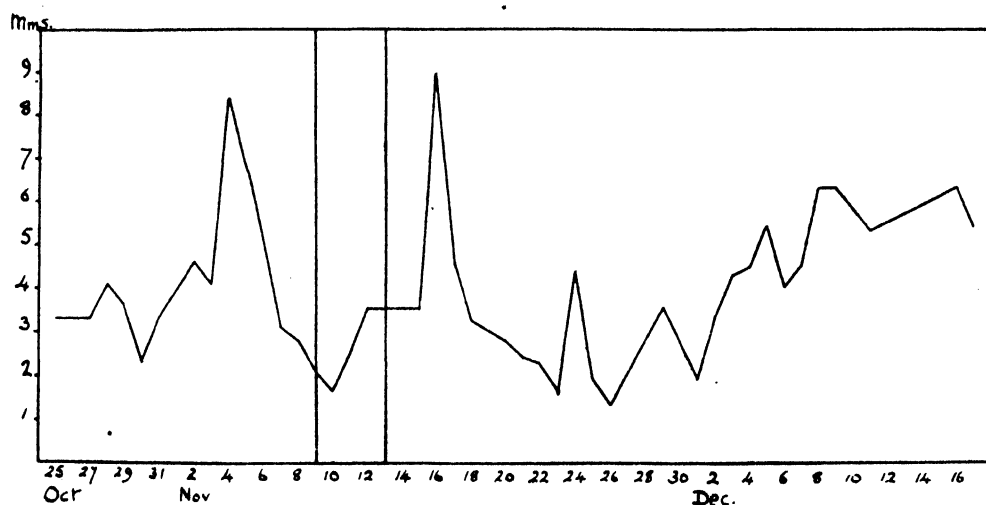


FIG. 15. Evaporation Measurements at Rio Observatory in mm. of water. The portion between the parallel lines is that covering the period of the transpiration test in the forest.

and thinner walled cells which appear to collapse in 95 per cent. alcohol. This I conceive to be the agent of the motion, achieved by variation of turgor relative to the passively turgid tissue on the lower side. Even granting this to be so, however, the cause of the movement remains unexplained. I have shown it to be unconnected with transpiration needs and I believe my observations show the night and day fluctuations of temperature at low levels to be too slight to account for it². The only remaining factor which appears likely to have a rapid influence is the presence or absence of light, and I would suggest that an explanation of the phenomenon of nyctitropism may be sought in reference to the presence or absence of osmotically active assimilation products, e.g. sugar, in pulvinar tissue readily sensitive to differences of turgidity, and so situated in the pulvinus that fluid changes

¹ In *Calathea* the leaves move upward at night.

² Darwin (1881) called temperature changes into play to account for the phenomenon.

in it would upset the mechanical balance of the tissue strains, resulting in movement. Though the explanation may prove to be of this order, the ecological significance of the movement remains unexplained, unless possibly it enables the plant to avoid the effect of the deposition and subsequent evaporation of dew on the lower surfaces of the leaves.

When, as we know from the work of Balls¹ with the stomatograph, plants exposed to strong sunshine may be prevented by rapid evaporation from opening their stomata and assimilating during the heat of the day, it is possible that the clogging of the stomata by moisture during the early sunshine of the morning, when assimilation should be active, would impose a disadvantage which the plant does well to avoid².

The motion of the leaves of ground herbs due to pulvinar action is of undoubted value in assisting them to catch favourable light and this may be the significance in all such cases.

3. **Comparison (continued): Morphological Types.** To return to the transpiration of the other leaves. The two lowest amounts were given off by the two leaves which would have been considered most different biologically—*Anthurium* and *Passiflora*. The leaf of the former was from a plant which hardly raised itself above the soil in deep gloom. To judge from the figures, it would seem that the young leaves are as incapable of effective transpiration as the leaves of the strongly heliophilous *Passiflora*, when introduced into like surroundings. If we incline to the view that the excessively low transpiration rate of some plants in this humid atmosphere must put them at a disadvantage in the matter of mineral salts compared with those species which manage to keep up a fair rate of water-passage, then it seems only logical to suppose that they must get a smaller supply of raw material from the soil, though they may continue to exist on what they get. We therefore would suppose that species capable of higher transpiration in an almost saturated air are better adapted to such an atmosphere than those which are not so capable. It remains to be seen however whether any directive adaptations towards this end are exhibited in the structure of the plants involved.

While on the question of functional differences between leaves it seems proper to call attention to the relatively larger amount transpired by the red leaf of *Acalypha*, which although also a sun plant seemed better able to carry on this function here than *Passiflora*. I shall have occasion later to

¹ W. L. Balls, "The Stomatograph," *Proc. Roy. Soc.* **85**, B. 1912, pp. 33-44.

² A similar hypothesis of the significance of nyctitropic movement of leaves was put forward by Stahl (1895), but his idea that the disadvantage of the deposition of dew on the leaf was its prevention of transpiration is inadmissible, partly on the showing of the above experiment and further with regard to the observations of Kohl (1886) and Wiesner (1876) that the wetting of leaves, where it has any effect, tends rather to increase the transpiration, the stomata absorbing the surplus water and thus opening more. But see Shreve (1914 a) for the contrary view of the wetting effect.

show that greenish light is a prominent constituent of the forest illumination, and I am inclined to regard the above result as attributable to the superior absorption of these rays by the red leaves with a corresponding rise of temperature and greater water-loss, a condition analogous in its way to that prevailing at depths of a few fathoms in coastal waters, where there are concordant assimilatory circumstances, with corresponding effects on the vegetation colouring. Indeed, in more than one respect a parallel might be drawn between conditions in the depths of a tropical rain-forest and in the sea. I put this colour-factor forward now as a suggestion in explanation of the *Acalypha* figures, though I consider differential absorption of light to be of much greater general importance in the matter of assimilation than of transpiration. The general characters of the leaves of jungle have been summarised by Schimper and by Lindman¹, and I can add but little to what they have said. The predominant form is everywhere lanceolate or lanceolate-ovate, entire, and either simple or compound-pinnate. The surface is in far the greatest number of cases glabrous and shining, and next in frequency, glabrous with a smooth lustreless surface. Hairy or woolly leaves occur, but only rarely, the outstanding examples being the Melastomaceae. Glaucous leaves occur in about 20–25 per cent. of the undergrowth species. Usually the leaves are dull green, but variegations of dull red and brown and occasional silvery leaves are not uncommon in the ground flora. The most frequent departure from the lanceolate form is among the lianes, whose leaves are often strongly cordate. Shrubs, also, have sometimes leaves with prolonged basal auricles, served by channelled veins, which seem designed to carry off the drainage water clear of the stem. This is the more necessary as the average daylight position of the leaves is obliquely upwards, thus throwing the drainage to their proximal end. This position is reputed² to render them less vulnerable to mechanical damage by heavy rain, but is just as conspicuous in the sheltered undergrowth of the forest as in species which are by stature or habitat generally exposed to that effect—never in any case very considerable in the American tropics.

The position seems rather an adjustment to illumination, analogous to that observable in sclerophyllous bushlands, but for reasons of weak rather than strong illumination—the effect being to expose both surfaces of the leaf to diffuse light and hence to increase the assimilating area. The leaf-mosaics are unusually perfect among undergrowth plants and the adjustment of the leaves to the varying angles of the sun's rays is very thoroughly effected by their petioles and pulvini. Pulvini may serve many ends by the movement of the leaves. I do not believe any single hypothesis can cover all the facts, but whatever may be the reasons, the need for leaf adjustability in the tropics has called into existence active pulvini throughout numerous families, in a degree quite unknown in temperate regions.

¹ Lindman (1906).

² Stahl (1893).

A beautiful example of leaf adjustment is to be found in the little fern *Cheilanthes radiata*. Every pinna of the frond is pulvinate and sets itself diaheliotropically with the utmost precision. Should the plant be unevenly lighted the effect of the irregularity is strikingly shown in the leaves, all the pinnae standing behind one another at the exact and appropriate angle, like good soldiers drilling.

The elongate apices known as "drip-tips," described by Stahl (1893) and considered by him as an adaptation to facilitate drainage of adherent rain-water, are plentiful and widely distributed among the plants which form the undergrowth of American jungles, though they have been more frequently examined by workers in the East, particularly in Java. It is impossible for me to criticise Stahl's conclusions as to the function of these "Träufel-spitze" in Java, where rain is much more violent and more frequent than in the western tropics; but I do not believe that in the region I am now dealing with they have the importance attached to them. Stahl held that it was an ecological advantage to a plant in jungle to be able to dry its surface quickly, avoiding the cooling effect of evaporation. This explanation has been effectively disposed of by Forrest Shreve (1914). The alternative suggestion is that of Jungner (1898), that rapid drying protects the leaf from colonization by epiphyllae.

Three arguments seem to me to tell heavily against this theory: (1) that the leaves are commonly held in an oblique position, points upward, in which case the drainage is of course reversed and runs to the proximal end: (2) that in the great majority of cases (70-80 per cent.) the "drip-tips" of mature leaves are withered and shrunken, or have dropped off: (3) that the possession of these points does not in effect protect leaves against the encroachment of epiphyllous plants, which occur thickly on some species of *Piper* possessed of these appendages¹.

What does seem to be of importance in hindering the attacks of epiphyllae is the quality of the leaf-surface. Leaves with a velvety or hispid surface are almost invariably free, and those with a highly polished surface nearly always. The leaves most commonly colonised are glabrous leaves with a smooth dull surface. Many of these bear a load of *Strigula* or species of *Lejeunea* which must interfere greatly with their ability to assimilate. If the surface moisture left on the leaf after rain favours the attacks of these plants, and it seems a reasonable view, then the immunity of velvety leaves is probably due to the rapidity with which they evaporate moisture, for it is readily observable that the leaves of *Echites pellatus*, which have such a

¹ This elongation of the leaf-tips is possibly a shade-effect, consonant with the elongation of the whole leaf which I have found to be well-marked in forest shrubs. A careful examination of the distribution of growth in developing leaves, under various conditions, would probably settle the matter.

surface, dry far more rapidly than the neighbouring glabrous leaves of other plants. The velvety surface increases evaporation, whereas the so-called "gutters" over the veins of some leaves rather tend to retain water unnecessarily by capillary action.

Rolled leaves are unknown in the true rain-forest, but at high elevations (over 1000 feet, in the dry or "secondary forest") *Cyperus* may be seen to roll its leaves at midday, in the way illustrated by the leaves of *Ammophila arenaria* on our own coasts.

Pendant young leaves, such as those of *Amherstia nobilis* in India, are decidedly rare, and I only observed them in one species of *Eugenia* among the shrubs of the forest, though Lindman figures a shoot of *Casearia* (Samydaceae) with pendant leaves from cooler forests further south. This pendant position has been interpreted as (a) protection against excessive light; (b) protection against drought¹. Some experiments made at Cambridge with young shoots of horse-chestnut, which have their leaflets deflexed in veneration, may shed some light on this.

Immature leaves severed from the plant lose water in the proportion of 1.78 to 1 of water lost by a mature leaf. One may therefore infer that they stand in greater danger of desiccation than mature leaves. This danger is checked in nature by the rapidity with which they draw water from the parent plant, for young (pendant) leaves were found to transpire, when still attached to their branches, in the proportion of 2.79 to 1 of water given off from an equal area of mature leaf.

That the pendant position does not give protection against high transpiration is shown both by the above figures and by the fact that two sets of young leaves, one in the natural pendant position, the other artificially held horizontal by wires, transpired in the ratio of 101.2:100, with the slight advantage to the horizontal leaves.

In the case of horse-chestnut then, the cuticular transpiration in the young leaf is sufficiently strong to swamp any protective effect that the pendant position may have upon the stomata.

Of course, *Aesculus* is not a tropical tree, but a native of Asia Minor, so that it may be objected that it is not a fair subject for comparison. In spite of this the dependent young leaves so strikingly recall those of some tropical trees that one is constrained to think that the ecological end served must be similar. Excluding water-loss as the cause, this pendency would appear to be attributable to the injurious effect of strong sunlight. Young leaves taken from shrubs in the forest and exposed to the full rays of a vertical sun under glass, even in a saturated atmosphere, are rapidly blackened and killed. Protection of some sort against this lethal effect is therefore certainly needed.

¹ Keeble (1895).

In Fig. 16 are some photographs of the prevalent leaf-forms of the shrubs and herbs forming the lower strata of the forest. The dominance of lanceolate or ovate-lanceolate forms over any others is marked. Next to simple, entire-margined shapes such as these, either with or without the long acute apices, the imparipinnate type, with leaflets of similar outline to the simple leaves, are commonest; while in the case of bipinnate leaves, the outline of the pinnae of the first order corresponds to the general outline of the simple leaves, even though these pinnae are themselves subdivided into pinnules.

4. **Transpiration under Laboratory Conditions.** A seedling of *Psychotria*, with roots, was fixed in a closed vessel of water and placed in a green glass case in the laboratory along with an open petri-dish of water, in order to compare the rates of transpiration and evaporation under approximate atmospheric saturation, when an undergrowth plant was deprived of most absorbable light and the advantage of an internal rise of temperature due to the absorption of light by the chlorophyll.

Transpiration progressed at about the same rate as in the forest experiment, namely, .00096 gm. per sq. cm. per hour, and evaporation at the rate of .0012 gm. for the same units, the relative humidity averaging 90 per cent.¹ for the whole period—96 hours. The whole plant gave off only 2.851 gms. of water for a leaf area of 30.96 sq.

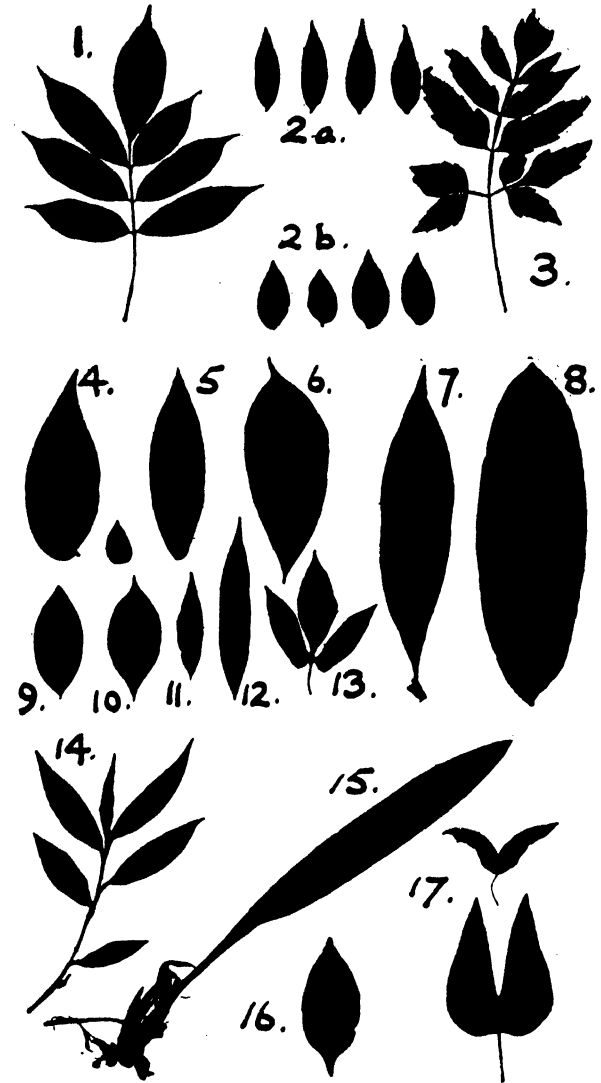


FIG. 16. Leaf Types from Forest Undergrowth. 1. *Sapindus*. 2. *Tradescantia*: a, Shade Form, b, Light Form. 3. *Serjania*. 4. *Begonia* spp. 5. *Piper*. 6. *Ocotea*. 7. *Dichorisandra*. 8. *Solanum*. 9. *Psychotria*. 10. *Melastoma*. 11. *Mapouria*. 12. *Eugenia*. 13. *Passiflora*. 14. *Panicum*. 15. *Anthurium*. 16. *Actinostemon*. 17. *Bauhinia* spp.

¹ Measured by a Lemprecht Polymeter, the only instrument then available.

cms. Considering the diluteness of the soil solution (see Section B) this can scarcely be considered adequate if it is regarded as the only means of obtaining the supply of mineral salts from the soil. We have also seen that the amplifying effect of the absorption of white light was negligible so far as the lowest plants of the forest are concerned, *Anthurium* for example transpiring less under normal forest conditions than the *Psychotria* which was deprived of assimilatory lighting.

Under the shade conditions of the experiment it therefore appears unlikely that a plant with a coloration complementary to green would be at any advantage in this respect, as the heating effect of supplementary light absorption, if any, would be extremely small; but it would gain an advantage in respect of assimilation. This remark does not apply, of course, to cases of sap-coloration dealt with before, such as that of the sun-plant *Acalypha*, but only to the red plastid coloration of certain shade leaves, which is essentially different from the anthocyan coloration of the young leaves of heliophytes. The latter is very likely a protective device, since tropical insolation can be very destructive to unprotected chlorophyll, as I have shown above in the case of forest leaves. This will be discussed at more length in Part II. Here only the effect of lighting on the transpiration is considered, and for these very low ranges of intensity it appears to be nil.

A comparison of the rate of transpiration from both surfaces of a typical and widely abundant forest sciophyte, *Calathea longifolia* (Marantaceae), was made in the following manner. The leaf, attached to a rooted plant in water, was gripped between the ground rims of two glass jars and the joints sealed with soft wax. In each jar was suspended a small tube of strong sulphuric acid to absorb the water given off, so that transpiration took place into dry air. The water-loss was as follows: upper surface $\cdot 00012$ gm. per sq. cm. per hour; lower surface $\cdot 00063$ gm., or 5.2 times as much as the upper surface. Thus, in this plant, one of the most pronounced sciophytes, purely cuticular transpiration is very slight in mature leaves as compared with stomatal. Indeed, it could hardly be otherwise, for many of the most typical sciophytes have quite a well-marked cuticle on their upper surfaces, and often upon the lower surfaces as well. This applies *a fortiori* to the shrubs and loftier plants. The paradox appears complete—plants living in a perpetually moist environment have protective arrangements against evaporation. Although the cuticle does not compare with the covering of truly xerophytic leaves it is perfectly well marked, and suffices to cause a predominance of glabrous, more or less coriaceous, leaves in the undergrowth. There is only one explanation that presents itself. Referring once again to the hygrographs taken in the forest (Figs. 6 and 7) it will be seen that their course during the day is interrupted by very numerous small irregularities, which I stated, on observation, to be the consequence of sun-flecks passing over the instrument. There are practically no portions of the forest floor possessing any autotrophic vegeta-

tion which are not reached by these flecks of sunlight and therefore subject to fluctuations of temperature and humidity arising from them¹. These may be very slight, but their effect would be to stimulate *individual* leaves to greater water-loss for short periods.

Shade leaves are very sensitive to slight diminutions of relative humidity. Leaves of *Echites peltatus* were tested, while still attached to the plant, with a porometer, and it was found that in a shaded laboratory, even with a humidity between 70 and 80 per cent., the stomata were completely closed. Now if such a comparatively small drop in the relative humidity affects the leaf to this extent, we may assume that it is the constant recurrence of such slight falls in relative humidity which has brought about the development of the protective arrangements of the leaf². Were the plant capable of even a slight degree of adjustment of water-flow such small changes would not have any adverse effect at all, and I feel it necessary to conclude that the undergrowth plants are incapable of such adjustment, even to the extent of very slight acceleration of the water current. If these plants, living in a continually moist environment, appear incapable of meeting a rise in the rate of transpiration without showing signs of flagging, indicated by the closure of the stomata, it *may* mean that their root absorption is strongly impeded by some edaphic factor.

Should anyone object that the protection above referred to may be brought about by seasonal changes of humidity rather than in the way suggested, it may be replied that according to the Observatory records published, the seasonal changes, even outside the forest, are on the whole so slight³ that the same argument, namely that the protection indicates a low power of root absorption, applies equally to this case. It is possible that both causes are contributory, while a third possibility is that the xylem supply of the individual leaves is very reduced, corresponding to the habitually low rate of transpiration.

5. **Leaf Structure and the Question of Adaptation.** On the general question of adaptation it seems desirable at this point to examine in detail the structure of some typical sciophilous leaves, from the aspect of transpiration capacity.

Firstly, in regard to the amount of intercellular space relative to the mass of the leaf.

The leaves of twelve species were examined, six typically sciophilous and six photophilous species from the same neighbourhood for comparison.

The results are given in vols. per unit weight (i.e. unit weight of leaf-

¹ The instrument recording the thermographs of the lower layers was intentionally protected from these sun-flecks, but the hygrograph was not.

² Francis Darwin points out that many plants close their stomata when brought from a greenhouse into a laboratory, but this in a temperate climate implies a much greater drop in the relative humidity than in the above case.

³ See Introduction, p. 13, under "Climate."

substance encloses the stated amount of air space) because weight is susceptible of much more accurate determination than area, and moreover by taking weight rather than area as a basis of comparison, differences in the total size and the texture of sun and shade leaves are neutralized, and the relation between mesophyll-substance and internal atmosphere brought out more clearly.

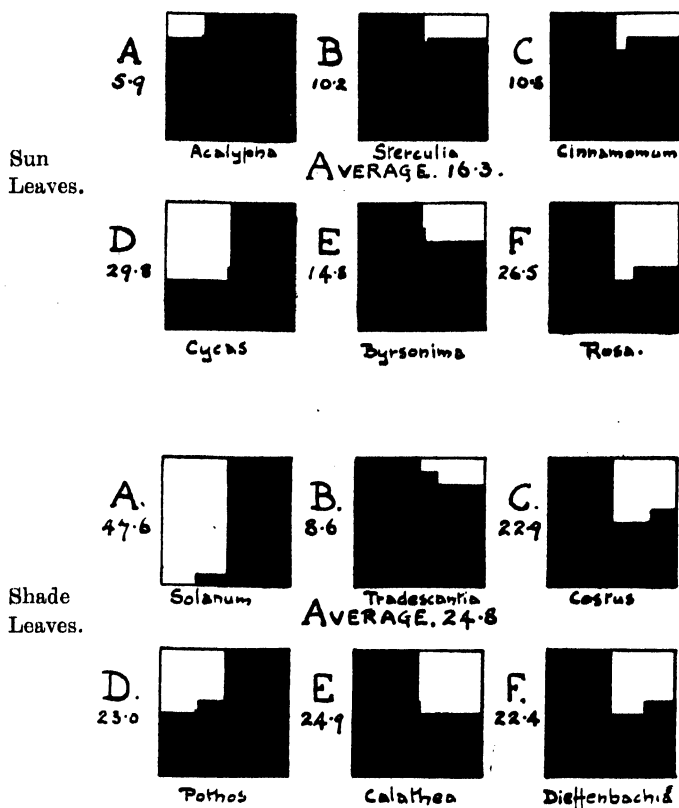


FIG. 17. Intercellular space per unit weight in sun and shade leaves at Rio. Each square represents unit weight of leaf substance, and the figures give the percentage of its total volume occupied by intercellular space.

Acalypha. Simple, broad, ovate, herbaceous.

Sterculia. Simple, lanceolate, coriaceous.

Cinnamomum. Simple, ovate, coriaceous.

Cycas. Multipinnate, coriaceous.

Byrsonima. Simple, lanceolate, coriaceous.

Rosa. Pinnate, glaucous, coriaceous.

Solanum. Simple, lanceolate, very large.

Tradescantia. Simple, lanceolate, succulent.

Costus. Simple, linear-lanceolate, long.

Pothos. Palmatifid, semi-succulent.

Calathea. Simple, lanceolate, coriaceous.

Dieffenbachia. Simple, lanceolate, coriaceous.

Leaves were injected under diminished pressure with a solution of alcohol of sp. gr. .99 (about 4 per cent. absolute) which is too weak to cause any shrinkage of the cells, but possesses a much lower surface tension than pure water and hence penetrates more easily. The probability that the stomata may close under diminished pressure is evaded by making slits in the back of the leaf. The volume of fluid absorbed is deduced from its weight,

making allowance for its specific gravity and temperature (23° C. in the Laboratory).

As one would expect, the absolute amount of air space in shade leaves is less than in sun leaves, their texture being thinner, but in proportion to their weight the case is reversed. The average amount of fluid absorbed *by unit weight* of the leaf is:

Sun leaves 16.3 per cent.

Shade leaves 24.8 „

It must be pointed out that the contrasted species were of widely different affinities so that no question of ecads is involved, but rather a widespread difference impressed upon totally different plants by a variation in environmental conditions.

For the sake of comparison estimates were made of some leaves at Cambridge, only in this case sun and shade leaves of the same species were chosen,

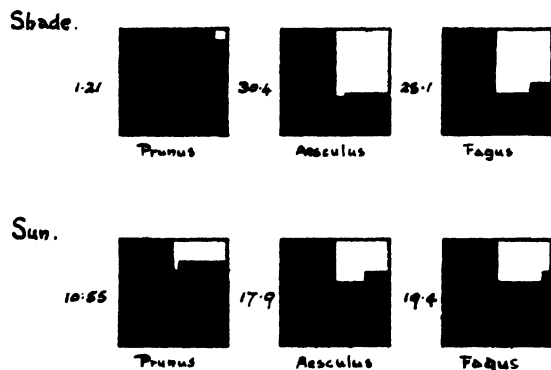


FIG. 18. Intercellular space in sun and shade leaves at Cambridge. For comparison with Fig. 17.

to illustrate the other aspect of the variation. The results bear out those obtained in Rio, the relative percentages being of closely similar order. I have not averaged these, because the aberrant 1.21 per cent. for the shade leaf of *Prunus* suggests that it was probably immature; but it can be seen that they resemble the Rio figures (see Fig. 17).

As a check to these estimations there are those given by Unger (1854), found by injection in a large number of temperate species. Excluding the figure 71.3 per cent. which was shown by an aquatic, *Castalia alba*, the average of his results is 20.64 per cent. He does not distinguish carefully the nature of the environment in which he found his material. If we lump my sun and shade leaves together in the same way the average comes out at 20.55 per cent.—strikingly close to Unger's. Nothing could better illustrate the uniformity of structural type in the Angiosperms than the correspondence of these figures, obtained in localities so far apart and from plants of environments so different in many important respects.

Increase in the amount of intercellular space implies an increase in the

relative amount of cellular surface exposed within the leaf. It is improbable that there is any absolute increase in the amount of surface exposed, for observation shows that in many of the shade leaves the spongy mesophyll is of great tenuity, there being scarcely any more cells than are necessary to ensure connection between the upper and lower surfaces. Two teleological explanations of this relative increase of exposed surface are possible; either *that it aids in increasing transpiration* or *that it plays a similar part towards CO₂ assimilation*. Both depend for their possible validity upon the capacity of the stomata for diffusion, and this we must proceed in the second place to examine.

Haberlandt (1904) gives the number of stomata per square millimetre on the leaf of the oak tree as between 300–400 on an average, and appends a table from Tschirch reproduced here, showing an increase in the average number of stomata for the more humid over the drier habitats:

<i>Plant</i>	<i>Habitat</i>	<i>Stomata per sq. mm.</i>
<i>Nymphaea alba</i>	Water	460 (Upper surface)
<i>Nym. thermalis</i>	"	625 "
<i>Quercus Robur</i>	Forests	346 (Lower surface)
<i>Quercus pedunculata</i>	"	288–438 "
<i>Prunus domestica</i>	Orchards	253 "
<i>Pyrus malus</i>	"	246 "
<i>Triticum sativum</i>	Fields	79 (Both surfaces)
<i>Avena sativa</i>	"	67 "
<i>Sedum acre</i>	Stony places	35 "
<i>Sempervivum tectorum</i>	Dry places	25 "

From these data it would be natural to expect large numbers of stomata in the habitat we are considering. This is not the case however. The following numbers are from the leaves of the commonest sciophilous species in my forest, representing twelve families:

<i>Phytolacca</i> sp., Euphorbiaceae	25 per sq. mm.
<i>Tradescantia discolor</i> , Commelinaceae	
Light form	38 "
Shade form	40 "
<i>Ficus rubiginosa</i> , Moraceae	50 "
<i>Costus spicatus</i> , Zingiberaceae	68 "
<i>Anthurium</i> sp., Araceae	88 "
<i>Mapouria tristis</i> , Rubiaceae	88 "
<i>Echites peltatus</i> , Apocynaceae	93 "
<i>Asterocaryum Airi</i> , Palmaceae	112 "
<i>Gomphia cuspidata</i> , Ochnaceae	130 "
<i>Solanum auriculatum</i> , Solanaceae	158 "
<i>Mimosa sepium</i> , Leguminosae	205 "
<i>Passiflora macrocarpa</i> , Passifloraceae	360 ¹ "

Now with the exception of *Ficus rubiginosa*, the leaves of which possess considerable water storage tissue, the above plants are almost exactly arranged in order of their average stature above the ground, as well as in ascending order of stomatal numbers, while none of them rival the numbers found in the typically mesophytic oak.

It would appear then that in these forests there is no increase in the

¹ This number is almost certainly too high, the leaf not being fully mature.

number of stomata corresponding, by the general rule, to the high humidity; that indeed there is a very marked *decrease* in their numbers, and this is opposed to the idea of adaptation for the furtherance of transpiration.

The herbaceous and low growing species given above almost all showed the "aquatic type" of stoma, associated with a high degree of humidity in the air surrounding them. That is to say, the pore is of slight depth, the "Vorhof" is suppressed and the "Hinterhof" rather large, while the guard-cells are either flush with, or even slightly raised above, the general surface of the leaf. The shrubs *Mapouria* and *Echites* have stomata of normal form with two vestibules, while it is especially worth remark that two of the species examined (*Asterocaryum Airi* and *Solanum auriculatum*), which usually reach to a height above the low shrub layer, have stomata surrounded by a conspicuous ridge, formed by the auxiliary cells, strongly suggesting a restrictive mechanism.

It is well known, however, that the diffusion capacity of the stomata varies according to their diameter, so that increased size might neutralize the apparent lessening of their numbers. With this in view the diffusion capacity of the leaf of one of the sciophilous species has been compared with the typically mesophytic *Helianthus*, for which full data have been made available by Brown and Escombe (1900). For this purpose the same species of *Anthurium* used in the transpiration test was selected, because, while possessing an average number of stomata, it showed the lowest rate of transpiration of the plants experimented with; and came moreover from the deepest shade¹.

In comparing the two leaves no account has been taken of the inter-cellular spaces. Although *Anthurium* has the thinner leaf its mesophyll is much more lacunar than that of *Helianthus* so that the absolute amounts of interspace are probably not far from parity.

The stomata of *Anthurium* are not of the aquatic type common among the ground plants, but are of a rather small normal type (total length, 34 micra) without a well-marked inner or outer vestibule and with a rather deep pore. The depressed transpiration might therefore, *a priori*, be laid to the charge of the stomata. The guard cells are almost, if not quite, chlorophyll free, though not on this account, as Lloyd (1908) has shown, to be regarded as incapable of movement. It seems difficult, however, to believe that movement can be occasioned by direct light in the habitat in which the plant is found. On this, however, I have no further information. (See Lloyd, 1908, p. 139.)

The stomatal pore when fully open measures 17×3 micra.

Depth of pore = 12 micra.

¹ As it never flowered I regret that it was impossible to identify it specifically, a common hindrance to work in the jungle, when a flora as vast and imperfectly known as that of Brazil has to be taken into account.

Brown and Escombe's¹ calculations of the diffusion capacity of the stomata in the leaf of *Helianthus* were based upon their well-known formulae, which I reproduce for the sake of reference.

In perfectly still air when diffusion shells are present on both sides of the stoma the diffusive capacity

$$Q' = \text{constant} \frac{A}{l + 2x} \dots\dots\dots(1),$$

and in air moving sufficiently to remove the outer diffusion shell

$$Q = \text{constant} \frac{A}{l + x} \dots\dots\dots(2),$$

where A = transverse area of the stomatal tube (assumed to be elliptical),

l = length of stomatal tube, .

and $x = \frac{\pi}{8} \times \text{diameter of a circle equal to } A$

$$= \frac{\pi r}{4} = .7854r, \text{ where } r \text{ is the radius of a circle of area equal to } A.$$

At the same time $A = \pi r^2$. Substituting in formulae (1) and (2) we get

$$Q = \text{constant} \frac{r^2}{l + .7854r} \dots\dots\dots(3),$$

$$\text{and } Q' = \text{constant} \frac{r^2}{l + 1.5708r} \dots\dots\dots(4).$$

If the pores are considered as elliptical, then

$$A = \pi ab,$$

where a and b are the semi-axes of the opening. And as $A = \pi r^2$ as well, then $\pi ab = \pi r^2$ or $r = \sqrt{ab}$.

Now Brown and Escombe found that the open pore of the stoma of *Helianthus* was equal in area to a circle having a diameter of 10.7 micra. Therefore $r = 5.35$ micra. The depth of the pore is 14 micra.

Substituting these in our equations (3) and (4) we find

$$Q' \text{ (still air)} = \text{constant} \times 1.275,$$

$$Q \text{ (wind)} = \text{constant} \times 1.57.$$

In the case of *Anthurium* the open pore has an area equal to that of a circle of diameter 7.14 micra (40 sq. micra) so that $r = 3.57$ micra. The depth is 12 micra. Substituting we get

$$Q' = \text{constant} \times .725,$$

$$Q = \text{constant} \times .86.$$

In other words the diffusion capacity of the *Anthurium* stoma in still air and in wind is to the capacity of the *Helianthus* stoma in the respective proportions of .57 and .548 to 1, or slightly over one-half the capacity of

¹ Brown and Escombe (1900).

the mesophyte. Moreover the ratio of $Q':Q$ for *Helianthus* is 1:1.23 but the same ratio in the case of *Anthurium* is only 1:1.19. That is to say, the stoma of *Anthurium* is not so effective for increase of diffusion by movement of the air, so that there is no evidence here of adaptation towards possible increase of transpiration.

Further, if we take into account the relative numbers of stomata present on unit area of each leaf, the capacities are still more disproportionate. *Helianthus* possesses 330 stomata per sq. mm. and *Anthurium* only 88. The diffusion capacities of leaves of the same area in the two species are therefore in the following proportions:

$$\begin{aligned} Q'. \text{ } & \textit{Helianthus} \text{ } 1. \text{ } \textit{Anthurium} \cdot 152, \\ Q. \text{ } & \textit{Helianthus} \text{ } 1. \text{ } \textit{Anthurium} \cdot 146, \end{aligned}$$

little more than *one-tenth* that of the mesophytic species. It still remains to find what relation the theoretical diffusion capacity of *Anthurium* bears to the actually observed transpiration values.

The value of the constant in the above formulae may be determined from Brown and Escombe's data, and thus the actual diffusion capacity of the leaf be found.

By comparison with *Helianthus* the constant is found to be .00000334, for a single stoma.

Inserting this in either formula (3) or (4) we may find the theoretical maximum of transpiration for either still or moving air. For comparison with the *Anthurium* transpiration readings, Q' , the capacity in still air, is the significant figure, for the transpiring plants in the experiment were sheltered by their position from almost all air-movement.

$$Q' = C \frac{r^2}{l + 1.5708r} = .00000334 \times .725 = .0213 \text{ gm. per sq. cm. per hour.}$$

The actually observed rate was, however, only .00032 gm. per sq. cm. per hour (p. 26), so that making all allowances for imperfect observation, the leaf of *Anthurium* has a theoretical capacity for transpiration over 50 times that which it normally exercises in its habitat.

Ewart (1905) has justly criticised all methods of measuring transpiration which involve the use of detached portions of plants, but the lengthy period over which the transpiration measurements were running tended to eliminate the effect of irregularities, especially as the check of free-water evaporation at the same time showed a close correspondence in fluctuation. In spite of the recognized defects of such an experimental method I am inclined to regard the measures obtained¹ as being, within a reasonable limit, the actual amounts of transpiration in this habitat under *almost maximal* climatic favourability, i.e. clear weather in the hot season.

This great excess of capacity over actual requirements puts any regulatory

¹ Compare also the amount given off by a *rooted* plant of *Psychotria* in a subsequent experiment.

function on the part of the stomata, short of absolute closure, out of probability. At the same time it renders it easily comprehensible how slight falls of relative humidity such as that due to the heating effect of a sun-fleck might lead to an enormous expansion in the water-loss. What plant could endure a sudden demand for an increase of even 500-1000 per cent. in its transpiration, supposing even that the ground water were unlimited? Moreover the diffusion capacity of *Anthurium* is not by any means the greatest among the plants examined. In *Solanum auriculatum* for example, the stomata are nearly twice as many (158 per sq. mm.) and only slightly smaller (32 micra, total length). With these facts in view the occurrence of protective devices in plants of the forest undergrowth is scarcely to be wondered at; for it follows that if the normal rates of transpiration are so low, the existence of a very high diffusion capacity must be a positive danger, unless (a) absorption and (b) conduction capacities are developed to correspond. Now if absorption was normally kept at a high level, then during shady periods guttation should be evident. Haberlandt (1891) attributed great importance to hydathodes on the leaves of undergrowth plants in maintaining a flow of water in conditions of high humidity (secretion-current) when the transpiration-current was almost or quite suppressed. In the absence of more direct means of encouraging the supposedly necessary transpiration this "adaptation" seems rather irrelevant. Guttation may occur in a few plants, but I can state with certainty that I never once observed it in the Brazilian forests although it was looked for under suitable conditions, and it cannot therefore be a general, still less a universal, phenomenon, while on the other hand the need for mineral salts, which on the accepted theory implies an equivalent water current, undoubtedly is. As there is no evidence to show that absorption can be rapidly augmented or decreased by any plants it seems justifiable to regard it as being, in these plants, normally if not permanently low, in correspondence that is to say with the normal low rate of water-loss, not with the exceptional high one.

A secondary factor controlling the supply of water to the leaves is (b) above, the degree of development of the conducting tissues, especially in the petiole. On this question Salisbury (1913) has published some interesting observations, but it has not been nearly as fully investigated as its importance deserves¹.

For comparison, leaves of three typical sun and three shade plants were investigated. The method employed by Salisbury for estimating the area of xylem in the petiole is very laborious and the following modification of it was adopted. Salisbury's method is extremely accurate, but this is much quicker and the inherent error in the method is overshadowed by the individual error of the leaves on any given shoot, which was shown by the above author to amount in some plants to as much as 22 per cent., even

¹ A correlation of the xylem in the petiole with the leaf area was first noticed by Guillard in *Adansonia*, 9, p. 107. Except for Salisbury's work this appears to be the only reference to it.

between leaves of comparable age. As this method enables the individual factor to be reduced by making possible the examination of a greater number of leaves any inherent lack of accuracy is practically negligible.

Choosing leaves of as nearly the same stage of development as possible, i.e. the youngest full-sized leaves on the shoot, the area of xylem in the cross-section of the petiole (half-way between the extremities) was estimated by tracing the vessels, stained with phloroglucin, by means of a camera lucida, under a magnification of 480 diams. Assuming the cross-section of each element to be a true circle the area is then found by measurement of the tracing and calculation. Few of the vessels in the petioles examined departed very markedly from the circular form, and in these cases the diameter was taken as the mean of the long and short axes—or in the case of vessels of very aberrant outline the area may be separately estimated by approximation to the nearest regular geometric form. This is confessedly only an approximation, but it is a very close one, and can be checked as regards probable error by the well-known method of comparative weights of paper areas. With the aid of a slide-rule the calculations can be done very rapidly. In any case the error only affects the absolute measurement, and does not invalidate the comparative figures which we are dealing with here.

The following were the measures obtained:

<i>Shade Species.</i>			
	<i>Area of Leaf</i>	<i>Area of Xylem</i>	<i>Ratio</i>
<i>Eugenia</i> sp.	18.3 sq. cms.	.0132 sq. mm.	13.9
<i>Mapouria</i> sp.	3.67 "	.0024 "	15.3
<i>Combretum</i> sp.	9.45 "	.0076 "	12.5
		Average ...	13.9
<i>Sun Species.</i>			
	<i>Area of Leaf</i>	<i>Area of Xylem</i>	<i>Ratio</i>
<i>Plumeria</i> sp.	3.37 sq. cms.	.0207 sq. mm.	1.63
<i>Anacardium</i> sp.	7.43 "	.059 "	1.26
<i>Luxemburgia</i> sp.	1.125 "	.0019 "	5.9
		Average ...	2.93

The ratios are taken as:

$$\frac{\text{Area of leaf}}{\text{Area of xylem} \times 100}$$

to bring them into correspondence with Salisbury's figures for the sun and shade forms of *Stachys sylvatica*.

The higher the ratio, naturally the smaller the amount of xylem developed per unit area of leaf. It follows that per unit area of leaf the sun leaves possess over *four times* as much xylem as the shade leaves, a discrepancy quite outside the limits of experimental error; which in any case was found by comparative weighing of the traced area, in the case which appeared to show the maximum number of irregularly shaped xylem elements, namely *Plumeria*, to be within 1.65 per cent.

The average area of the sun leaves was less than that of the others, and the petioles of all were short (.5—1 cm.) so that the development of extra hadrome purely for mechanical support does not complicate the results.

The leaves of the sun-plants used were all of a decidedly coriaceous type, and it might be argued that the protection afforded by the mechanical adaptations of cuticle, etc., reduce the transpiration in such leaves to such a slight amount that it would be quite fallacious to consider the extra development of petiolar xylem as indicating a higher transpiration capacity. Bergen (1904) has, however, shown clearly that sclerophyllous "xerophytic" leaves transpire strongly, and the mature leaves more so than the young ones. The increased xylem may be justly regarded, on this basis, as implying an increased capacity for transpiration.

The idea that there is a connection between the amount of xylem in the petiole and the transpiration from the leaf is obscured by the uncertainties of transpiration measures taken from isolated leaves, which hinder, when small differences are involved, a direct demonstration of relationship.

In Salisbury's attempted proof the leading assumption upon which he bases his argument is that the area of a leaf is proportional to its transpiring power, for he says: "If, however, such a definite relation does not exist the results here obtained are inexplicably constant."

This being the case, Salisbury's final contention may be expressed as a formula:

$$\frac{\text{Area of leaf}}{\text{Area of xylem}} = vt,$$

where v is a constant, and t = the transpiration, in the given plant.

One of the species examined by him was *Stachys sylvatica*, sun and shade forms being compared. He gives a table, to summarize which shows that the average ratios of xylem to leaf area for the sun and shade forms are in the proportion of 1 : .93, i.e., the shade leaf is only slightly worse off for xylem supply than the sun leaf. Accepting the accuracy of these figures it is only on the basis of the assumption spoken of above that Salisbury's conclusion can be accepted, namely, that the equalization of xylem supply shows an equalization of the transpiring capacity of the shade leaf to that of the sun leaf. To do so, however, leads to this inconsistency:

Let A = area of the leaf, and a = area of the xylem.

Then in the sun leaf:

$$\frac{A}{a} = vt,$$

and in the shade leaf:

$$\frac{A'}{a'} = vt';$$

now if

$$\frac{A}{a} = \frac{A'}{a'}, \text{ then } t = t',$$

or the sun transpiration equals the shade transpiration, which is not the case. It appears, therefore, that there is no such constant as v .

As it is impossible to estimate with sufficient accuracy the actual transpiration of a given individual leaf, we are prevented from making what would otherwise be a direct and conclusive comparison. The transpiration of mature leaves is so preponderatingly stomatal rather than cuticular, that an estimate of the capacity of the stomata for diffusion might however be taken as representing the transpiration capacity of the leaf as a whole. Such an estimate is easily possible by means of the formulae presented by Brown and Escombe, and although it does not represent the actual transpiration, any more than does the area, yet it is more certainly in proportion to it, inasmuch as the maximum transpiration of certain plants is already known (Brown and Escombe, 1900 *a*) to bear a definite relation to the total diffusion capacity of the stomata. Furthermore it is a constant quantity for each leaf, independent of experimental conditions, unlike the transpiration itself.

In order to ascertain these relationships leaves of *Syringa vulgaris* and *Aucuba japonica* have been investigated at Reading. As these both have opposite leaves it is easy to check the individual variation by comparing a pair of leaves, which can be assumed to be of the same degree of maturity. Plants were chosen growing wholly in the shade and wholly in the sun, the photometric ratio between the two habitats being ascertained to be as 1:55; and pairs of leaves were chosen, the youngest of full size on their respective shoots.

Before the leaves were cut from the plants, pieces of the lower epidermis were stripped off and immediately fixed in absolute alcohol to preserve the stomatal form for subsequent measurement. Lloyd (1908) has experimented very critically with this method and came to the conclusion that so long as adherent portions of the mesophyll were absent from the pieces of epidermis, the absolute alcohol dehydrated and thus rendered inelastic the stomatal guard-cells too quickly for any measurable change of form to take place. If the stomata are subsequently moistened with water contraction will occur, as the guard-cells have already been plasmolysed by the alcohol, but so long as the epidermis remains in an anhydrous medium the form of the guard-cells will remain unchanged. By means of this very convenient method it is possible therefore to compare the relative apertures of stomata under diverse conditions with ease. Only in cases where there is marked abnormality in the form of either guard-cells or epidermal cells is a serious change of shape during dehydration to be apprehended, and neither of the plants employed are thus abnormal.

The results are given in the table, Fig. 19.

The most striking result is the disparity between the two sorts of leaves in *Aucuba* as compared with the close similarity in *Syringa*. This points to the inference that the biological difference between the sun and shade positions

is more accentuated in winter than in summer, so that the evergreen leaves are more influenced than the deciduous summer leaves. The sun leaf of *Aucuba* has a higher diffusion capacity than the shade leaf, but its xylem supply is proportionately still greater. If we figure to our minds the higher demand for evaporation made upon an insulated leaf under cold conditions with a decline in root absorption, it is not difficult to comprehend the causes which control this result.

The xylem supply per unit area of leaf is less in the shade leaf in both cases, but it is most noteworthy that in both cases, while the diffusion capacity is somewhat less in the shade leaf the proportion of the area of xylem to it is very much less, so that if it be accepted that there is any direct connection between the development of petiolar xylem and the transpiration, then the shade leaves are worse provided for in this respect than the sun leaves; indicating a probability that the actual maximum transpiration is a smaller

	Area=a	Diffusion Capacity=d	Xylem area=x	$\frac{a}{100x}$	$\frac{d}{x}$
<i>Aucuba</i> Sun.	32.7 sq. cms.	.706 ccs. per hr.	.1092 sq. mms.	3.0	6.95
Shade.	26.5 "	.535 "	.0344 "	7.7	15.5
<i>Syringa</i> Sun.	29.1 "	1.25 "	.122 "	2.38	10.25
Shade.	18.9 "	.934 "	.076 "	2.41	12.3

FIG. 19. Vasculation of sun and shade leaves compared. For explanation of figures see text.

fraction of the theoretical maximum in the case of shade leaves than in the case of sun leaves even in a temperate climate—a probability which is borne out by the obvious relation of shade to increased humidity, and is indeed adumbrated by the results of the *Anthurium* experiments. As the theoretical diffusion capacity is only slightly decreased (1: .75) in the shade leaves, the actual transpiration of these leaves may be held to be capable of considerable theoretical expansion. The lower proportion between the xylems (averaging 1: .47) precludes however advantage being taken of this possible expansion, a fact which is incompatible with the view of adaptive increase of transpiration in the shade form¹.

Lastly, there is in these cases no constant proportion between area and diffusion capacity.

From the above considerations it appears that in the shade leaves of the forest both the power of root absorption and the development of conducting

¹ Assuming for the sake of illustration, on the basis of the *Helianthus* observations, that the xylem of the sun leaf is just capable of transmitting water to one-sixth of the full diffusion capacity, the xylem of the shade leaf is only capable of transmitting approximately one-tenth.

tissues are decidedly sub-normal, and incommensurate with the relatively high diffusion capacity of the leaves. This being so the latter has the semblance of a possible danger to the plant rather than an adaptation to assist transpiration; emphasising the need for cuticular and occasionally stomatal protection, which as we have seen exists even among the undergrowth plants, and leaving them open to the risk of occasional desiccation.

If then the existence of a high stomatal diffusion capacity in the shade leaves cannot be referred to increase of transpiration, and in view of the poor supply of water to the leaf tissues may even be an awkward matter under incidental circumstances, we are bound to the same view with regard to the dependant factor of increased intercellular space; and, in attempting to explain this curious condition of affairs, it is now necessary to consider it in the light of the second alternative which we set out to examine (see p. 38), its bearing upon assimilation. If the diffusion capacity is needlessly high from the point of view of transpiration, we are justified in asking why it is as high as it is.

Assimilation is a primary function, about the paramount importance of which there is no dispute, and it is undeniable that the poor illumination of jungle undergrowth must seriously interfere with it.

The amount of CO₂ in ordinary air being so small the amount of light effective in full sunshine is also small, the CO₂ being the limiting factor. It follows, therefore, that illumination may be considerably reduced without in any way affecting photosynthesis, but that still further reduction of light beyond the limit exactly necessary for the assimilation of the normal amount of CO₂ results in curtailment of photosynthesis, even if the CO₂ is increased, the light being now the limiting factor.

It is not intended to go into a full discussion here of the assimilatory relationships. This is reserved for Part II, but the functions are too closely involved to be considered in a wholly separate fashion.

The light in the shade of the jungle is about .007 of the full sunlight outside (compare the ratio 1:018 in the experiment on *Syringa* and *Aucuba* in this country), that is the shade close to the ground, but not directly under foliage. In the densest shade, which is only inhabited by saprophytes, there is too little light to be measured by ordinary photometric means. The content of CO₂ in the air is higher than normal (see Part II) but this would have no effect upon photosynthesis under ordinary internal conditions of the leaf, the light being the limiting factor.

Brown and Escombe have shown¹, however, that under ordinary circumstances the diffusion capacity of leaves is in excess of their power of assimilation, the factors which limit the latter function being the imperfect absorbing power of the mesophyll and the small amount of CO₂ in the air. This implies the presence of an excess of light.

¹ Brown and Escombe (1902).

In the present circumstances all these factors are precisely reversed. The illumination is often insufficient, while the supply of CO_2 in the air is excessive, largely owing to the rapid decay of organic substances consequent on high temperatures. These are beyond the plants' control—but what happens in regard to the factors within that control?

The diffusion capacity should, we would conceive, be at least as high as in mesophytes, in order that under such difficult conditions a greater supply of CO_2 might be rendered to the mesophyll. But the functions of diffusion and absorption are so interdependent, that without an increase of the latter the diffusion inwards of more CO_2 would be without value. If we look within the leaf we find three features which can be interpreted as augmentative of absorption: the chlorophyll is more exposed to the incident light than in mesophytes, the mesophyll cell-walls are extremely thin, and lastly the aforementioned factor of a relative increase in the amount of cell surface exposed to the air in the interspaces of the mesophyll. It might be considered that if the above is a correct view of the case there should be an absolute as well as a merely relative increase in the lacunae, but the obvious objection to this is the feeble light, which is incapable of penetrating more than five or six cell-layers, so that absolute increase in the bulk of the mesophyll, i.e. in the actual thickness of the shade leaves, would be quite ineffective in augmenting assimilation.

Assuming then for the time being that the absorptive capacity of the mesophyll cells is increased, we would expect the diffusion capacity of the stomata at least to have remained constant, if not to be increased. What we actually find is a reduction. Now looked at from the point of view of transpiration we found ourselves constrained to ask why the diffusive capacity was so high—while from this aspect it is its reduction that demands explanation. It appears to me that this can only be accounted for by the suggestion that we see in this the interaction of two opposed forces—assimilation and transpiration, and the endeavour on the part of the plant to effect an impossible compromise. The increase of the power of assimilation is, as I think everyone will admit, the primary need of plant life, but its unlimited development is everywhere checked by the counterbalancing effect of water-loss, which even under these extreme conditions appears solely as a hindrance to assimilation, not as a necessary function encouraged in adversity by any structural adaptations on the part of the plant.

Even if the transpiration check were altogether removed and indefinitely large quantities of CO_2 diffused into the leaf it is very doubtful if the plant could make up by improved absorption for the light deficiency¹, but no such opportunity is permitted it, and as a consequence it is certain that if under-

¹ Even though there be a supernormal amount of CO_2 in the air of the forest this affords no explanation of a reduced diffusive capacity, as there must exist a *theoretically* unlimited demand for CO_2 .

growth plants depend upon ordinary photosynthesis for their supply of organic material, they must suffer from a grievous deficit.

Granting then that the need for increased assimilation is real and that the increase of interspaces in the leaf can be interpreted on these grounds, the interpretation may be reasonably accepted as genuine, since we have shown on other grounds that it is not explicable in terms of transpiration.

(c) TRANSPIRATION AND THE INTAKE OF SALTS.

1. **Possible Relations between Transpiration and Salt-Intake.** So far the transpiration problem has been considered only on its own merits without reference to its significance in the plant's nutritive processes. Apart from hydration, an ancillary function of the transpiration current has always been held to be that of introducing an adequate supply of mineral salts in solution into the plant from the soil.

This opinion does not, however, establish a causal connection with transpiration. The maintenance of a strong water current through the plant implies not only a low aerial humidity but also plentiful soil water, in the absence of which a dry atmosphere leads simply to xerophytic conservation of water. It is then perfectly conceivable that in the presence of abundant soil water which we have just postulated as essential to strong transpiration the increased dilution of the solutions available to the plant may compensate for the amount absorbed, tending to limit the actual quantity of salts entering the tissues. Apart from this there is, however, the experimentally observed fact that plants growing in dilute solutions tend to absorb relatively more water than salts, so as to lead to a gradual concentration of the remaining liquid. Although much attention has been directed in the past to this question, yet in almost every research too much attention has been paid to the atmospheric conditions and too little to the soil and absorption factors, which are capable of invalidating the results obtained in a manner largely unrecognized.

The most illuminating experiments which I know of are those of Hasselbring (1914) carried out in Cuba. Plants of tobacco were grown in iron tanks in the same soil. They stood close together under exactly similar conditions in everything except that one tank and its contents were shaded from direct sun by cheese-cloth stretched upon a frame. Each day the tanks were weighed and the quantity of water lost replaced in each. When the plants reached maturity they were compared in regard to dry weight, ash weight, and total amount of water absorbed, the results being as follows:

In the open	Dry weight	188.42 gms.
	Ash weight	18.25 gms.
	Water absorbed	46344 ccs.
	Water absorbed per gm. of ash	2548 ccs.
In the shade	Dry weight	188.14 gms.
	Ash weight	21.08 gms.
	Water absorbed	36187 ccs.
	Water absorbed per gm. of ash	1718 ccs.

The plants which transpired the most possessed the smallest ash-content, and conversely the plants with reduced transpiration obtained equivalent weights of ash for less water absorbed than did the plants in the sun. Not only was a large transpiration current no guarantee of a high ash absorption, but a lessened current did not necessarily imply inadequate mineral supply.

Many persons have held the view that liquid diffusion is adequate to account for the migration of salts in plants, without reference to transpiration; while Haberlandt has at different times laid stress upon the action of hydathodes and of intercellular osmosis as the controlling factors when transpiration is undeveloped, implying however that increased transpiration must

Shade leaves, Ash weight and water of hygroscopicity per 1 gm. of dry weight.

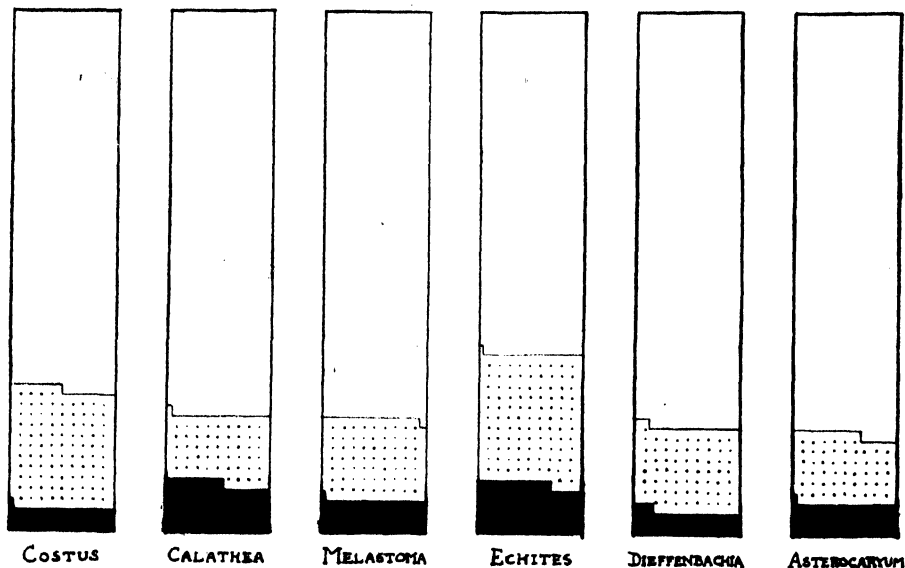


FIG. 20. Ash and hygroscopic water in shade leaves per gram of dry substance. Each area = 1 gm. From the base to the top of dotted portion = water. Black portion = Ash.
Costus. Simple, long-lanceolate. *Echites*. Simple, cordate, velvety.
Calathea. Simple, lanceolate, coriaceous. *Dieffenbachia*. Simple, lanceolate, coriaceous.
Melastoma. Simple, ovate, hairy. *Asterocaryum*. Multipinnate, coriaceous.

assist the process, a belief that does not seem to be borne out by Hasselbring's experiments. The latter's results seem to show that the plant exercises powers in root-absorption which may quite override the diminished effect of transpiration and may perhaps be called into play by the depression of the latter process, or reversed by its augmentation in view of the small amount of mineral matter actually demanded and the inconvenience that might attend its accumulation internally.

A close investigation of the relation between transpiration and salt absorption throughout the periods of a plant's life-history would be valuable and interesting, as affording light on the theory of their correlation.

2. **Comparison of Ash-Contents.** I have not been able to undertake

any investigation of the absorption relationships in jungle undergrowth, but I have examined the ash weights of certain leaves from sun and shade positions. The results are shown in Figs. 20 and 21. Each of the large areas represents 1 gram of dry material and the blackened portion the corresponding amount of ash.

Sun leaves. Ash weight and water of hygroscopicity.

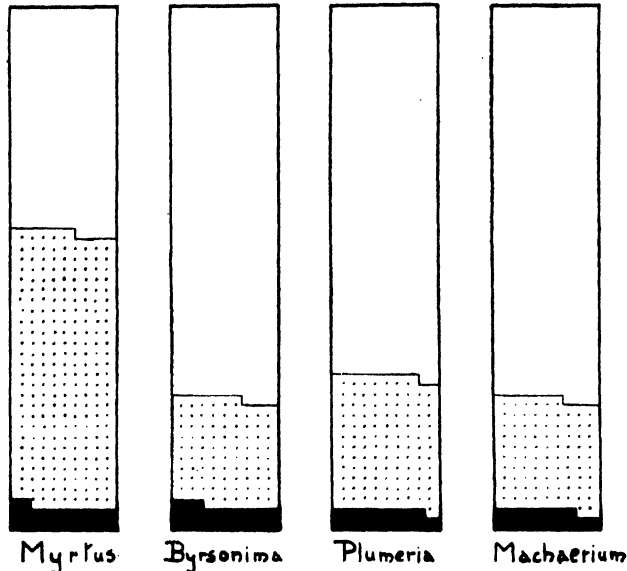


FIG. 21. Ash and hygroscopic water in sun leaves. As in Fig. 20.

Myrtus. Simple, coriaceous, small.

Plumeria. Simple, lanceolate, coriaceous.

Byrsonima. Simple, lanceolate, coriaceous.

Machaerium. Pinnate, ovate, hairy.

The proportion of ash in the dry weight is greater, it will be seen, in the shade leaves than in the sun leaves. This does not, nevertheless, imply a higher total content, since there is no doubt that the proportion of dry weight to total wet weight is smaller in the case of the shade leaves¹.

Thus although it is possible that the ash weight may be even lower in

¹ The dry weight of the shade plants in Hasselbring's experiment was only minutely less than that of the sun plants.

The following figures, illustrating these relations in the case of two plants of a temperate habitat, were obtained by examination of the same plants of *Syringa* and *Aucuba* which were employed for a previous investigation:

<i>Syringa</i>	Sun	Shade	<i>Aucuba</i>	Sun	Shade
Wet weight	100	100	Wet weight	100	100
Dry "	35.5 = 100	23.4 = 100	Dry "	31.5 = 100	26.5 = 100
Ash "	2.3 = 6.5	2.2 = 9.4	Ash "	1.43 = 4.55	1.05 = 3.95

Comparing the sun and shade plants of *Syringa*, the drop in dry weight is greater than the drop in ash weight, bearing out the contention in the text; but in *Aucuba* this is reversed, the proportional drop in ash weight being greater than that in dry weight.

The difference in ash-proportion in this case (3.95—4.55) is not so great however as it is in the reverse direction in *Syringa* (9.4—6.5).

relation to the fresh weight in the case of the shade leaves, yet the fact remains that it is high in proportion to the dry material, which alone represents the assimilatory activity of the plant, so that there is no evidence to show that the plants concerned suffer from mineral starvation. Indeed from this point of view the shade plant appears to be better off than the heliophyte¹.

Still, with a lowered dry weight the sciophyte may be compared to a dilute solution—all solid portions being more tenuous and more fully permeated by imbibed water. That this condition may in part facilitate the diffusion of mineral salts through the tissues is very probable; though whether this alone is sufficient or whether there are other causes contributory, to be looked for in roots or soil, one cannot at present state.

3. Hygroscopic Condensation in Leaves. Shreve (1911) has shown that the Hymenophyllaceae of the Jamaican forests when surface dry and subjected to a very moist atmospheric environment, are capable of absorbing water hygroscopically, much in the same way as do lichens and mosses. In the case of these latter plants the water thus imbibed by the cell-walls is probably transmitted to the protoplasm and augments what may else be a scanty supply.

I have tried to ascertain whether an analogous power is possessed by the phanerogams of forest undergrowth. (See Figs. 20 and 21.)

The material, dried at 100° C., when placed in a moist chamber certainly absorbed a considerable amount of water, but this amount bore no positive relation either to the amount of the dry matter itself, or to the ash-content, or even to the sun or shade habitat, but seemed capricious. Most probably it depended on the physical structure of the dry matter rather than its mass, a relationship eluding direct observation. It does not seem, at any rate, to have an ecological significance for the shade plants, although it is slightly more prominent in the heliophytes, which would be considered *a priori* more in need of any aid to maintaining moisture in their leaves.

The experiments of Ganong (1894) and others controvert the possibility of water in significant quantities being absorbed through the leaves. This is true in so far that water absorbed hygroscopically cannot take the place of water absorbed through the roots, but water absorbed hygroscopically may, under xerophytic conditions, augment the total water supply.

One specific instance of the utility of hygroscopic water occurs in *Cecropia*. The fat-bodies produced from cushions at the base of each petiole develop only in moist air, and not in dry, even though the stem be plentifully supplied with water. This is attributable to the hygroscopic action of the cuticularized hairs which cover the pulvinar cushions with a dense, velvety indumentum, through which appear the delicate fat-bodies upon which the ants feed.

¹ A rather curious phenomenon, which it is difficult to account for, was observed in these ash estimations. The soil on which the sciophytes were growing is derived from underlying bright-red ferruginous laterite. The ash of four out of six species was of the same brick-red colour.

DETAILED SUMMARY OF PART I. HUMIDITY.

Section A. Atmospheric Humidity.

1. Under the peculiar climatic conditions prevailing within the undergrowth of tropical rain-forest, practically isolated from the influence of external changes, there is in general very slight transpiration and a correspondingly low rate of aqueous evaporation.

2. The leaves of plants growing in such conditions possess a maximum diffusion capacity which bears a very much higher ratio to the actual rate of transpiration, as measured under conditions favourable to it, than in the case of mesophytes. The possible increase of the diffusion capacity by wind is (in one case at least) less than in the mesophytic *Helianthus*.

3. Both absorption and conduction capacities are developed only on the low scale.

4. The leaves show no adaptation calculated to aid in extending their transpiration towards the limit of capacity. On the other hand they are commonly protected by cuticle and other means against excessive water-loss¹.

5. The leaves of undergrowth plants are subjected to frequent short periods of insolation by "sun-flecks." These lower the humidity markedly where they fall. In conjunction with this must be taken the facts that such rays have a greater intensity and a correspondingly greater power of evaporation than in temperate climates, while the chlorophyll in the leaves of shade plants is more exposed to their influence than in habitual heliophytes.

6. The above reasons show how the foliar evaporation may for short periods rise above the low capacity of the plants to supply water. Hence arise the protective devices shown even in this very moist habitat.

7. Shade leaves have a greater internal surface relative to their mass than sun leaves. This does not appear to be a transpirational adaptation, but as the illumination is very slight, it may be better interpreted as a means of increasing the CO₂ absorption capacity, the percentage of carbon dioxide in the forest air being supernormal.

8. It has been found that the average of intercellular space in leaves examined in Brazil corresponds closely to that found in Europe. This may be associated with the constancy of leaf function over the whole world and the corresponding constancy of atmospheric constitution.

9. Lack of capacity to increase the transpiration current under the stimulus of sun-flecks, wind, etc., leading to the necessity of protective devices, seems to point to edaphic factors antagonistic to absorption.

10. Under such conditions of depressed transpiration a shortage of

¹ Wiesner's statement (1893), that under *similar* conditions shade leaves transpire more than sun leaves is no evidence that there exist devices for encouraging transpiration in shade leaves such that under normal *differentiated* conditions they would transpire in the same proportion. Hasselbring's experiment indeed shows that this is not so.

mineral matter might be anticipated. Examination of ash shows, however, a higher content, relative to the total weight of assimilates, than in heliophytes.

11. This is taken to indicate that the absorption of mineral salts is independent at least of foliar evaporation, the almost complete suppression of which is thus seen to be of only secondary importance to the plant.

12. Whether the suppression of foliar evaporation signifies the suppression of a water current in the axis does not appear. It is not impossible that a slow current is maintained by root-pressure, enough to satisfy the demands of elastic growth and of CO_2 assimilation, which between them utilize the major portion of the water supply, some part of which also returns through the phloem or may eventually be excreted in the fluid state.

In such circumstances the measurement of water-loss would give no indication of the absorbing capacity of the plant, of which it would be quite independent.

ON THE ECOLOGY OF THE VEGETATION OF BRECKLAND

By E. PICKWORTH FARROW.

VII. GENERAL EFFECTS OF BLOWING SAND UPON THE VEGETATION.

(*With Plate II.*)

WHEN the effects of small sand blasts upon the vegetation were discovered¹ observation was kept for any other effects which blowing sand might have upon the vegetation.

The blowing of sand seems to be a general phenomenon in many parts of Breckland. It has already been mentioned that when once a sand blasted area is started it tends to spread. Apparently the bombardment of the sand grains which are already moving tends to start other previously stationary sand grains moving and these in their turn tend to start still others, and so on, until a large sand blasted area may be produced.

In the case of these large sand blasted areas there is frequently a cliff of sand at the edge of the denuded sand blasted area furthest from and facing the prevailing wind and sand blast. (See Photos 1 and 2, Plate II.) Beyond the edge of the cliff the higher surface is occupied by vegetation, and the soil consists of tougher strata bound together by plant remains and not yet disintegrated by the sand blast.

Apparently the wind and sand blast on the surface tend to cut away the upper strata of the sand more and more as the length of sand blasted area exposed to the prevailing wind increases. This sand is transported beyond the furthest edge of the sand blasted area, and piled up in this position in the form of a new cliff or dune the face of which in its turn gradually becomes disintegrated by the continued sand blast. The sand blasted area thus gradually increases in length in the direction of the prevailing winds as the face of the cliff is progressively disintegrated.

The accumulated moving sand grains from the increasing depth of sand blasted surface in front of the cliff strike against the face of the cliff and gradually cut it away. (See Photos 1 and 2.)

The height of the cliff above the adjoining sand blasted surface gradually tends to increase both by the increasing removal of the surface strata of the adjoining surface by the sand blast and by the deposition of sand carried

¹ See this JOURNAL, Part VI, 6, pp. 144—152

by the wind and sand blast on to the upper surface of the bordering cliff. Later on the sand cliff becomes sufficiently high to check the sand from being carried by the wind and sand blast up its face and deposited on the upper surface beyond, and after this the face of the sand cliff often does not increase greatly in height above the surface of the adjoining area. The wind transported sand then accumulates at the base of the cliff instead of being carried up to and deposited on the upper surface beyond. Often however this loose transported sand which would otherwise tend to accumulate at the base of tall sand cliffs is removed from this position by winds different in direction from the prevailing winds but not in themselves sufficiently powerful to remove new sand or originate strong sand blasts and new sand cliffs. Some of this loose sand is subsequently again dashed against the face of the cliff by the prevailing winds and some of it is carried to the upper surface.

Thus in the case of long sand cliffs when the wind strikes them at an angle, and in the case of isolated portions of sand cliffs when sand can escape round their edges, transported sand does not accumulate extensively at their bases and especially in these cases the faces of the sand cliffs often eventually come to project a considerable height above the adjoining surface of the neighbouring sand blasted areas owing to the greater and greater removal of the surface strata by the sand blasts, and owing to the deposition of some of the wind borne sand on their upper surfaces. (See Photo 2.)

A gradual upward sloping tendency of the ground in relation to the prevailing wind probably assists in the formation of sand cliffs. This view is supported by the fact that when the retreating face of a formerly fairly tall sand cliff reaches the downward sloping edge of a slight valley and retreats down the sloping valley side the cliff often gradually becomes obliterated.

Especially in the cases of fairly tall cliffs, their faces generally become undercut by the sand blast. This, no doubt, is largely owing to the roots of the vegetation which occupies the upper surface of the cliff tending to hold together for a time the associated sand grains lying immediately below the upper surface while the lower portions of the cliff, relatively free from roots, and also subjected to a far more powerful sand blast owing to being nearer to the sand blasted surface, are more readily cut away by the sand blast. This undercutting of the faces of sand cliffs by the sand blast is well seen in Photo 1. The undercutting is often assisted by the presence of rabbit burrows running beneath the surface.

As a result of the undercutting of the faces of the cliffs the upper portions of the cliffs which hold together for a time often come to overhang the basal portions very markedly. (See Photo 1.)

Eventually however, when the undercutting has proceeded sufficiently, the overhanging upper portions break away and fall to the bases of the cliffs where they are ultimately disintegrated by the sand blast. Such debris of *Calluna* plants, etc., fallen to the bases of the sand cliffs and being gradually

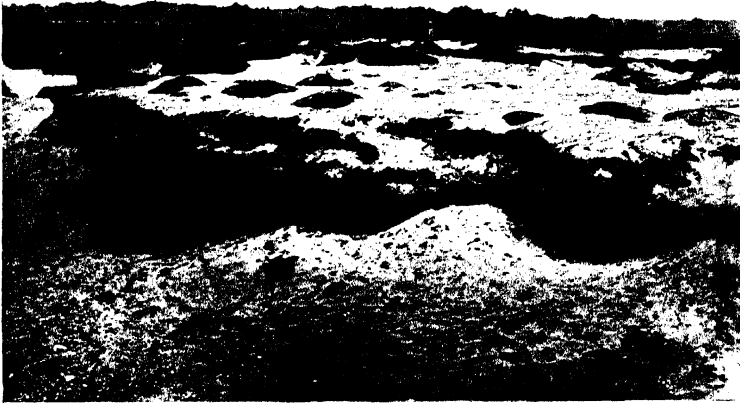


Photo 1. UNDERCUT FACE OF A SAND BLASTED BRECKLAND SAND CLIFF ON THE FURTHEST EDGE OF A SAND BLASTED AREA FACING THE PREVAILING WINDS. Note the undercutting caused by the sand blast across the lower surface. When this undercutting has proceeded sufficiently portions break away and fall to the lower surface where the debris are ultimately disintegrated by the sand blast. Note fragments of *Calluna* etc. produced in this way on the lower surface. Note sand on the upper surface carried there by the sand blast. Many plants can rise through this deposited sand, thus reoccupying the new surface as indicated by the dark streaks in the Photo (see p. 62). For the bearing of this on Richtofen's theory of the origin of Loess see p. 63. Note the remains of the original layer of vegetation submerged by the deposited sand and now exposed on the disintegrating face of the cliff about six inches below the present surface: also the blow-outs in the face of the cliff on the extreme left.

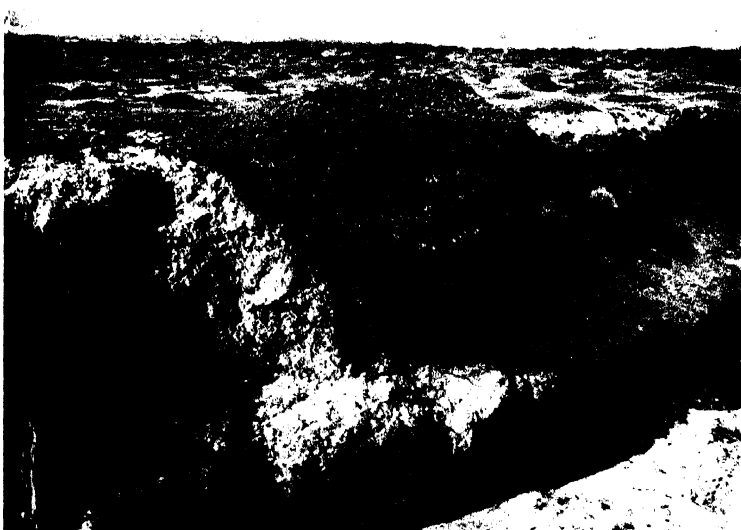


Photo 2. LARGE RABBIT-GRAZED *CALLUNA* HUMMOCK BENDING OVER THE RETREATING FACE OF A SAND BLASTED SAND CLIFF AS THE LATTER GRADUALLY BECOMES DISINTEGRATED. Note the fissures produced in the surface of the hummock as it bends over the disintegrating and retreating face of the cliff (see p. 57). Eventually the hummock will fall upside down on the sand blasted lower surface and will become disintegrated (see p. 57). Note that the lower portions of this cliff project further and resist disintegration better than the upper portions. This is because the lower portions represent the original surface strata long occupied by vegetation and cemented together by humous products, whilst the upper portions represent wind blown sand comparatively recently deposited which is looser and more readily torn away by the sand blast.

disintegrated by the sand blast, can be seen under the overhanging edges of the cliffs in Photo 1.

Partly undercut *Calluna* plants on the upper overhanging edges of disintegrating undercut cliffs often hang suspended by their roots after some of the upper overhanging portions of the cliff have broken away. Sometimes these suspended *Calluna* plants live for a time in this position, but their suspending roots are eventually released by the continued disintegration of the faces of the cliffs and the suspended plants eventually fall upside down on the sand blasted surface and the debris is ultimately disintegrated. In some instances a number of dead *Calluna* plants upside down and partly buried in sand with their roots projecting in the air can be seen on the sand blasted lower surface at a distance of several feet from the present face of a disintegrating sand cliff. In these instances no doubt these dead *Calluna* plants hung upside down suspended by their roots on the face of the cliff until these suspending roots were released by the continued disintegration of the cliff and the dead *Calluna* plants were deposited on the sand blasted surface in their existing positions before the face of the cliff retreated several feet to its present position.

Sometimes large rabbit-eaten *Calluna* hummocks on the edges of disintegrating sand cliffs bend over the edges of the cliffs as the latter become disintegrated, the formerly closely aggregated branches of the hummocks separating and showing fissures on the surface as the hummock bends over the edge of the retreating face of the cliff, as can be well seen in Photo 2. No doubt the remains of the large rabbit grazed and rounded *Calluna* hummock seen in this photo will eventually fall upside down on to the lower surface and the debris will ultimately be disintegrated by the wind and sand blast. As mentioned above fragments of the roots and stems of disintegrated *Calluna* plants can be well seen on the lower surface of the cliff shown in Photo 1.

In some cases *Calluna* plants on overhanging edges of the undercut cliffs die a long while before these undercut portions break away and fall to the bases of the cliffs, although all the other *Calluna* plants on the upper portion of the cliff are alive. Probably the porous soil and relatively dry climate of Breckland are in themselves not particularly favourable to *Calluna*, a plant of oceanic climates, and it appears very probable that the death of *Calluna* plants on the overhanging edges may very likely largely be due to exposure of many of the roots and reduction of the already small available water supply by the undercutting.

In some cases the main roots of *Calluna* plants on greatly undercut upper portions of cliffs reach down from these undercut upper portions and remain fixed in the surface strata below although the sand which formerly surrounded a great part of their length has been torn away by the sand blast. In these cases the *Calluna* plants on the overhanging edges often remain alive although they may be greatly undercut by the sand blast, and no doubt this is owing

to the fact that, although they are so greatly undercut, they can continue to obtain a sufficient water supply through the roots, which, although partially exposed, remain fixed in the substratum.

It is interesting to note that *Calluna* stems on the immediate edges of greatly overhanging cliffs and now relatively inaccessible to rabbits are frequently comparatively tall and flower vigorously, while the stems of all the other *Calluna* plants in the vicinity, which are comparatively easily accessible to the rabbits, are nibbled closely down by them and are entirely prevented from flowering.

It has already been mentioned that the sand cliffs on the furthest edges of sand blasted areas tend to increase in height above the adjoining sand blasted surfaces both by removal of the original upper strata of these surfaces by the sand blast and by the deposition of some of the removed sand on the upper surfaces beyond. Such wind blown sand comparatively recently deposited upon the original surfaces beyond the edge of the cliff can be well seen on the exposed faces of the sand cliffs shown in Photos 1 and 2. In most cases these old surfaces were long occupied by vegetation (*Calluna*, etc.) and the strata just beneath them exposed on the faces of cliffs are usually much darker in colour than the strata of the comparatively recently deposited sand above them owing to being stained dark by the humus products of the original vegetation which existed for a comparatively long time upon them. (See Photo 2.)

In consequence of this longer occupation of the original surface by vegetation the sand grains of the exposed strata lying just beneath the original surface are partly cemented together by the resulting humus products and thus these strata are considerably tougher than the strata of the comparatively recently deposited sand above them. As a result of this greater toughness of the strata lying just beneath the old surface, these strata when exposed on the faces of disintegrating cliffs often resist the disintegrating effect of the sand blast better than the more recently deposited upper strata of sand although they are nearer to the adjoining sand blasted surface. In consequence of this the lower strata (often themselves with undercut edges) frequently come to project further on the faces of sand cliffs than the more disintegrated upper strata of comparatively loose recently deposited sand, as can be well seen in Photo 2. Thus the cliff may come to consist of two stages or tiers, each separately undercut.

Sometimes a particular upper surface of the comparatively recently deposited sand remains stable and uncovered by additional wind blown sand for a time, and when this happens—if the upper surface remains uncovered by additional sand for a sufficient period—it frequently becomes colonised by *Calluna*. Later on this *Calluna* which had colonised the relatively stable upper surface often becomes covered by subsequent wind blown sand, and ultimately the remains of it appear on the disintegrating face of the cliff

as a thin stratum of decaying *Calluna* stems, etc., embedded in the sand at some distance below the subsequent upper surface, as can be well seen in Photo 1.

Much of the sand which has accumulated at the edge of the sand blasted area is often carried up through "blow-outs" in the faces of the cliffs and deposited on the upper area. Blow-outs in the face of a cliff can be seen on the extreme left-hand side of Photo 1. The face of the cliff seen in this photograph is gradually retreating across the downward sloping side of a slight valley and, largely in consequence of this downward slope of the surface, the cliff itself is gradually becoming obliterated.

In some instances the sand blast has already cut away nearly all of the former cliff in certain positions, except where portions remain as hillocks on the leeward side of masses of vegetation (principally *Calluna* hummocks) which have protected them from the sand blast. This effect of *Calluna* hummocks, etc., on the faces of disintegrating sand cliffs in protecting the portions of the cliffs lying just behind them from the disintegrating effects of the sand blasts reminds one of the action of *Suaeda fruticosa* bushes on mobile shingle banks in protecting the areas of shingle lying just behind them from the deposition of shingle in the rolling over of the surface of the bank during on-shore gales¹. It is interesting to note that behind *Suaeda* bushes gullies are left whilst behind *Calluna* hummocks exposed to sand blasts hillocks are left. The sign of the effect of the protective action on the contours is reversed in the two cases. Much sand is usually carried along the blow-outs which exist between the protected remains, and becomes deposited on the vegetation beyond. Some areas of the sand blasted and deposited sand usually become colonised by *Polytrichum piliferum* except just beyond the blow-outs themselves where the surface is far too mobile for any sort of colonisation to occur.

Various phenomena strongly confirm the view that the faces of the relatively tall sand cliffs are homologous with the much more dwarf but frequently undercut faces of the much smaller sand cupolas and hummocks previously described²: the undercut faces of small vegetated cupolas and the faces of much taller vegetated sand cliffs are produced by the sand blast in the same manner, the one kind of projecting cliff face being a much larger variety of the other. The tendency towards the production of blow-outs through which the sand can escape in the case of long tall cliffs and the frequently resulting production of isolated portions of cliffs is probably the same tendency which results in the production of the small isolated cupolas around which the wind borne sand can escape, for the edges of a small cupola in the directions of varying winds may be

¹ Oliver, F. W. and Salisbury, E. J., "Vegetation and Mobile Ground as illustrated by *Suaeda fruticosa* on Shingle." This JOURNAL, 1. 1913, pp. 261-264.

² See this JOURNAL, 6, 1918, pp. 144-152; notably Photos 2, 4 and 5, Plates III. IV and V.

regarded as the edges of an almost infinitely wide blow-out in the face of a dwarf cliff.

The sand carried up the face of the cliff is deposited amongst the vegetation on the higher ground beyond and any *Calluna* hummocks on this upper surface are often almost, and sometimes completely, filled with this wind blown sand. (Notice the sand in the *Calluna* hummocks on the upper portions of the cliff in Photo 1.)

In the case of rabbit grazed *Calluna* hummocks this wind blown sand is first deposited on the windward side of the hummocks (see Photo 1). This is interesting, for in the case of developing sand dunes the sand is chiefly deposited on the leeward side where the wind velocity is lowest. The difference probably arises because the *Calluna* plant has much denser vegetation than that of a developing sand dune, so that this denser vegetation can sufficiently reduce the wind velocity even on the windward side for the sand to be deposited there and remain at rest. The rabbit grazed and rounded *Calluna* hummock in Photo 2 which is bending over the edge of the cliff as the latter gradually becomes disintegrated contains much wind blown sand.

Sometimes owing to the distribution of a sand blast tending to increase when once it has started great masses of sand are eventually cut away and extensive areas are bared. The general lack of vegetation on the surfaces in these cases is due to the surface sand blast and the mobility of the surface and is not due to excessive dryness, for these bare surfaces of sand are at a lower level and nearer to the underlying chalk than were the formerly stable upper surfaces which have been cut away and which were occupied by vegetation until the denuding sand blast cut them away. In the case of these large sand blasted bare areas the sand blasts sometimes become dormant for a time, and when this happens these formerly sand blasted bare areas gradually become recolonised. *Polytrichum piliferum* is the pioneer coloniser in these cases and is normally followed by *Cetraria aculeata*, *Cladonia coccifera* and *Ceratodon purpureus*.

It was thought that it would be interesting to have further information about the colonisation of bare sand and in order to obtain this the sand of a metre quadrat of grass heath was dug out to a depth of half-a-metre and removed and the space was filled with sterile sand carted from below a bare area. This quadrat for studying the colonisation of bare sand is inside the large rabbit-proof quadrat¹ and is protected by boards at its sides to prevent the loose sand from being blown away (middle quadrat in Photo 1, Part IV).

The bare sand in this experimental quadrat became colonised very rapidly by *Rumex acetosella* seedlings and a few months after it had been constructed there were very many of these on the quadrat. There were also some *Senecio vulgaris* seedlings and some wind blown *Cladonia* spp. on the sheltered edges near the boards. Several *Taraxacum erythrospermum* seeds were also found

¹ See this JOURNAL, 5, 1917, Plate XVII, Photo 1 in Part IV.

on this quadrat in the autumn after it had been constructed. In the spring there were many *Teesdalia nudicaulis* plants and the *Taraxacum erythrospermum* seeds germinated and produced seedlings. Many *Galium saxatile* seedlings also appeared and being here protected from rabbits later on flowered profusely. One solitary *Cytisus scoparius* seedling appeared. Possibly the seed of the last named may have been carried and deposited by a bird.

It will thus be seen that the bare sand of this experimental quadrat is becoming colonised very rapidly. Most of the plants which are colonising this experimental quadrat are much taller than the dwarf mosses and lichens which are colonising the larger exposed formerly sand blasted bare areas already referred to. Probably the greater height of the plants on the experimental colonisation quadrat is chiefly owing to their being protected from attack by rabbits, but no doubt the relative absence of sand blasts may also have something to do with the matter. The bare sand of this experimental quadrat which is protected from rabbits is also becoming colonised much more rapidly than the exposed bare sandy areas. No doubt this is chiefly owing both to the absence of direct attack by the rabbits on the colonising plants and to the proximity of established plants protected from rabbit-attack inside the rabbit-proof enclosure which produce many more inflorescences and flowers than if they were exposed to rabbit-attack and can thus supply seed to the colonising area more quickly. Photographic records are being made to determine the relative rates of colonisation.

It has already been stated (see pp. 55 and 56) that when the sand blast has cut a cliff in the sand at the furthest edge of a sand blasted area, sand is usually lifted by the sand blast up and over the edge of this cliff and deposited upon the higher surface beyond. Sometimes fairly thick layers of sand are deposited in this way upon the upper surfaces, but sometimes the lifted sand is deposited as a thin mantle of sand over the vegetation on the upper surfaces. Frequently the vegetation of considerable areas is covered by a deposited mantle of sand in this way--sometimes for a distance of several hundred yards behind the edge of the cliff. These areas appear almost bare of vegetation for a time owing to the superficial deposit of wind blown sand.

In all of these cases however it was noticed that the areas on which the vegetation had been completely covered quickly became again occupied by vegetation--so quickly indeed that it seemed impossible to account for the reoccupation of these areas on any hypothesis of simple re-colonisation.

In order to see more exactly what happened and in order to have definite information about the date of the deposition of the sand, a metre quadrat of grass-heath inside the large rabbit-proof enclosure was boarded off to prevent the sand from being blown away and sterile sand was then carefully sifted in and on the vegetation of this boarded metre quadrat to a depth of 5 cms. above the previous surface. (Left-hand quadrat in Photo 1 of

Part IV¹.) The average height of the vegetation on this quadrat was about 2 cms. and its maximum height at that time was about 3 cms., so that all the grass-heath vegetation on this quadrat was completely covered by the 5 cm. deposit of sand and was mostly covered to a depth of 3 cms. In spite of this, the sterile sand covering the previous vegetation quickly became occupied by vegetation and at the end of two months the vegetation on the quadrat was quite as luxuriant as the vegetation on the untouched quadrat and many inflorescences had appeared. On examination it was found that the rapid recolonisation of the new sandy surface was owing to the vegetation which had been submerged by the deposit of sand rapidly sending up fresh shoots to the new surface and thus covering it again.

Many plants in Breckland have been found to possess this power of sending up shoots through a superficial deposit of sand and thus reaching the fresh surface. *Agrostis vulgaris*, *Festuca ovina*, *Festuca rubra*, *Galium verum*, *Rumex acetosella*, *Thymus serpyllum* and *Lotus corniculatus*, along with many others, were found to behave in this way.

The details of the process vary somewhat in the case of different plants. In the case of *Agrostis vulgaris* the main stem usually elongates, quickly grows up through the deposited sand and produces a fresh set of leaves at the new surface; but sometimes lateral stems also grow up, and adventitious roots are soon produced by the new stems. In the case of *Festuca ovina* several lateral stems usually rise through the sand deposit and produce fresh leaves at the new surface. These rising lateral stems often produce small etiolated leaves inside the deposited stratum and later on they also produce adventitious roots inside this stratum. *Lotus corniculatus* usually sends up a number of thin etiolated lateral shoots from the buried crown, and when these rising shoots reach the top they each produce fresh groups of leaves at the new surface and eventually adventitious roots are produced inside the sand. In the case of *Lotus corniculatus* these rising lateral shoots also produce etiolated leaves and etiolated secondary lateral shoots inside the sand stratum before reaching the surface.

It thus appears that many plants—by means of sending up fresh shoots to reach the new surface—possess the power of contending with such an apparently unfavourable environmental influence as being covered over with sand. *Ammophila arenaria* and other sand grasses have long been known to have very extensive powers of this kind, but it is becoming apparent that very many other plants have similar powers. *Suaeda fruticosa* also can contend with rising shingle and can rise through it by the production and growth of lateral shoots². This method of contending with rising shingle is very similar to the general method by which all these other plants

¹ This JOURNAL, 5, 1917, Plate XVII.

² Oliver, F. W. and Salisbury, E. J., "Vegetation and Mobile Ground as Illustrated by *Suaeda fruticosa* on Shingle." This JOURNAL, 1, 1913, p. 259.

can contend with rising sand, and the general process is one of considerable interest.

This phenomenon may be rather important in connection with Richthofen's theory of the mode of origin of the loess¹, for this theory requires the subaerial deposition and stabilisation of ultimately considerable thicknesses of material. Since so many plants can rise up through subaerially deposited material, vegetation may well have greatly assisted in the subaerial deposition and stabilisation of ultimately great thicknesses. Probably the structures which Richthofen observed in the loess and termed "roots" were really continuous stems which had continually risen up through the successive strata of subaerially deposited material as it was deposited. Prof. Marr informed the writer that it did not seem that the long continuous structures which pass through considerable thicknesses in the loess could possibly have been formed by "roots" and this was one of the difficulties in Richthofen's theory of the mode of origin of the loess. If however these structures instead of being "roots" which had penetrated down were formed by continuous stems which had continually risen *up* through successive strata of subaerially deposited material, this difficulty in Richthofen's theory of the mode of origin of the loess would be explained.

In this connection much of the sand of Breckland—in any case for considerable distances behind certain sand cliffs—is a sort of subaerially deposited loess. Digging on many of these areas reveals stratified sections of the successively deposited sand layers frequently each about 1 cm. thick and long remains of the shoots with adventitious roots of various plants which have continually risen up through the successively deposited sand layers.

The vegetation of the quadrat upon which sand was deposited became quite as luxuriant and even closer than that of the untouched turf. The deposited sand probably had some bad effects on the vegetation but it seems to have had some good effects which have quite compensated for any bad effects. In this respect, these grass heath plants resemble many other plants such as *Suaeda fruticosa* and *Ammophila arenaria* at Blakeney, for these plants are often stimulated when shingle or sand is deposited around them. The effect is in some respects contrary to what might have been expected. It is not known definitely how this unexpected result is brought about, but perhaps it may be partly due to the older parts which have become buried deeper decaying and becoming available as manure for the new upper tissues which have been produced. It has apparently been found generally economical in nature for old tissues to die and to be replaced by new and vigorous tissue and it may perhaps be possible that the increased luxuriance which is often apparent in these cases may be partly due to a modification or speeding up of the life-death-life cycle.

There are doubtless many other instances in which plants contend with

¹ Richthofen, F., "On the Mode of Origin of the Loess." *Geological Magazine*, 1882.

unfavourable environmental influences by producing new vertical shoots to rise to the new surface. The writer observed some good instances of this at Blakeney, where individual plants of *Glyceria maritima* were surrounded by a dense growth of *Obione portulacoides* which was gradually increasing in height. When this happened the *Glyceria* plants sometimes sent up new vertical shoots to the upper surface of the *Obione* layer, where they produced fresh sets of leaves which remained connected with the smothered leaves and the substratum by means of the new vertical shoots. These instances resemble in many ways the process by which other plants contend with rising sand, but in the case of *Glyceria* contending with rising *Obione* well-developed adventitious roots are not produced by the new *Glyceria* shoot as they are when a plant has risen through deposited sand.

RECONNAISSANCE OF THE PLANT ASSOCIATIONS IN THE NEIGHBOURHOOD OF NEWBURY, BERKSHIRE

BY GEORGE MORRIS.

(*With a Sketch-map and Geological Section.*)

THE observations recorded in the following brief notes were made by a party of fifteen, as part of the work of the Regional Survey Conference at Newbury during the second week of April, 1917. The examination of the associations was necessarily superficial, but it may be worth while briefly to set down the results as a record of the distribution of vegetation in a part of England which has not been described in detail from the ecological standpoint, and also as indicating the scope and use of holiday meetings for regional study by teachers, students and amateur ecologists. In general the distribution of associations and their relation to the geological formations correspond very closely with the accounts given in *Types of British Vegetation*, to which references are made in the footnotes.

The area dealt with is based on the chalk syncline, striking east and west, which extends from the scarp of the North Hampshire and Wiltshire Downs on the south, where a sharp fold occurs (see Section, Fig. 1), to the scarp of the Berkshire Downs, forming the southern boundary of the Thames Valley, on the north. Along this syncline the Kennet and its tributary the Enborne flow from west to east, dissecting the Tertiary beds which lie in the hollow of the syncline into a series of east-and-west parallel ridges, capped by Plateau Gravels of Post-Tertiary age. North of the Lambourn, which flows into the Kennet from the north-west, outliers of the Tertiaries, again capped by Plateau Gravels, and separated by smaller tributaries or dry tributary valleys, occupy the dip-slope on the northern limb of the syncline, while the higher levels of the chalk are largely covered with "Clay-with-Flints." The area also includes small inliers of Upper Greensand between the Tertiaries and the southern escarpment. The rivers are bordered by alluvium, and by strips of river gravel which form terraces on each side of the alluvium (Map, Fig. 2).

GEOLOGICAL FORMATIONS AND PLANT ASSOCIATIONS (Map, Fig. 2).

Chalk. Where exposed on the dip-slopes the chalk is almost entirely under the plough, with ruderals and weeds of cultivation forming the flora of the roadsides and field boundaries. Individual species such as *Daucus*

carota, *Poterium sanguisorba* and *Cnicus acaulis* indicate the remains of a chalk grassland flora. The chalk of the escarpments, e.g. of the Inkpen scarp south of the Kennet, and of that overlooking the Vale of White Horse, is covered with a close turf¹ of *Festuca ovina* with numerous chalk-pasture plants such as *Thymus serpyllum*, *Origanum vulgare* and *Cnicus acaulis*. Beech hangers, with occasional *Buxus* and *Taxus*, were noted on both escarpments².

Clay-with-Flints. The red Clay-with-Flints on the dip-slopes of the chalk is also mostly arable land, but with numerous plantations of pine and beech, serving principally as game shelters. On the Inkpen ridge a small *Calluna-Ulex* community was observed and its relation with the chalk grassland noted.

Upper Greensand. The inlier of this formation, exposed by the denudation of the fold on the southern edge of the syncline (see Section, Fig. 1), was almost entirely under permanent pasture, but a small hazel coppice with a vernal flora of *Adoxa*, *Scilla* and *Primula acaulis* was noted.

Tertiary Beds. These are exposed on the flanks of the ridges and outliers north and south of the Kennet, and form a densely wooded area. They consist of alternating Woolwich and Reading Beds (sands, gravels and clays), London Clay, and Bagshot sand. The sands and gravels bear dry oak-birch woodland (*Quercus robur* dominant with *Betula pubescens*) and a ground vegetation of *Rubus*, *Pteris*, *Oxalis acetosella*, *Digitalis purpurea*, *Teucrium scorodonia*, etc.³ Mixed deciduous woods, either entirely planted or formed by the introduction of planted species into the natural woodland, also occur. The principal constituents are *Quercus robur*, various exotic species of *Quercus*⁴, *Fagus sylvatica*, *Pyrus aria*, *Acer pseudo-platanus*, *Betula*, with *Pinus silvestris*,

¹ *Types*, p. 173.

² *Ibid.* p. 163.

³ *Ibid.* p. 92.

⁴ *Q. sessiliflora* was looked for but not found.

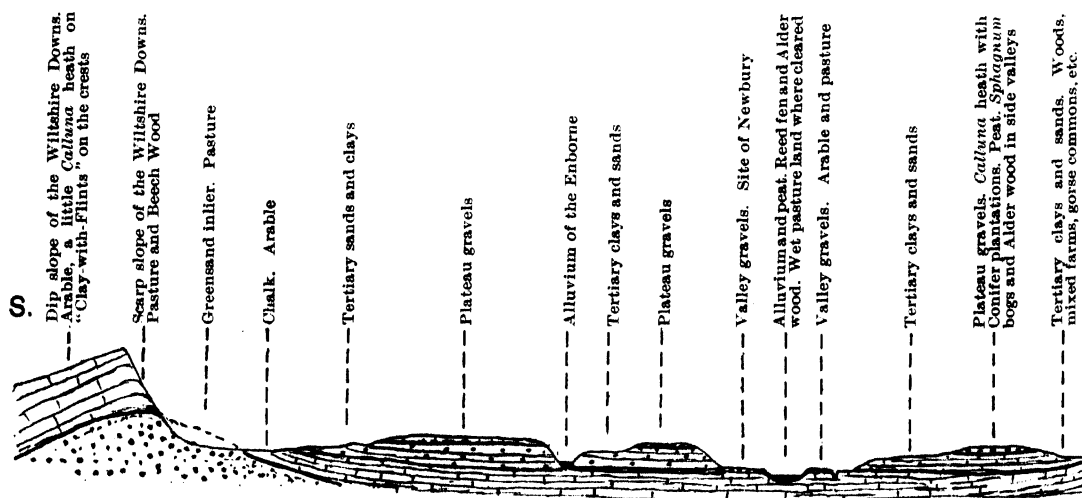


FIG. 1. Generalised section (not drawn to scale) across the Kennet

Abies alba and other exotic conifers. The ground vegetation resembles that of the natural oak-birch type. There are also plantations of conifers with a distinctly heathy flora passing into the dry oak type when more mature. When a dry oakwood or mixed wood on the same soil is cleared for planting conifers, the old ground vegetation of *Rubus*, *Pteris*, etc., appears to give place to a heath flora in which *Calluna*, *Erica cinerea* and *Aira flexuosa* are dominant in dry places, with almost pure *Molinietum* on the borders of the alder swamps, while *Sphagnetum* tends to form in the undrained wet areas. Seedling birches are very abundant in these clearings and probably have to be removed to prevent their smothering the young conifers.

The clays bear damp oakwood dominated by *Q. robur* with coppiced *Corylus* and *Primula acaulis*. *Ranunculus auricomus*, *Luzula pilosa*, *Euphorbia amygdaloides* and *Mercurialis perennis* (often locally dominant)¹.

The valley bottoms bear alderwood (*Alnus glutinosa*) with *Ficaria verna*, *Chrysosplenium oppositifolium*, *Spiraea ulmaria* and *Urtica urens*².

Plateau Gravels. These are characterised by typical *Calluna* heath³, which was seen in all stages of development from an open association of seedlings two or three years old with lichens, *Polytrichum juniperinum* and *Rumex acetosella*, to a state in which degenerating *Calluna* bushes are covered with *Cladonia*. The succession seems to be constantly set back as the result of frequent heath fires. The following variations of the heath were noted: (a) grass facies with *Prunus spinosa* and *Rubus* scrub, in the lower parts of the valleys and where oakwood approaches the heath⁴; (b) *Calluna-Ulex* passing to pure communities of *Ulex europaeus* and *U. minor*⁵; (c) enclosed areas planted with species of pine, and with birch seedlings invading the

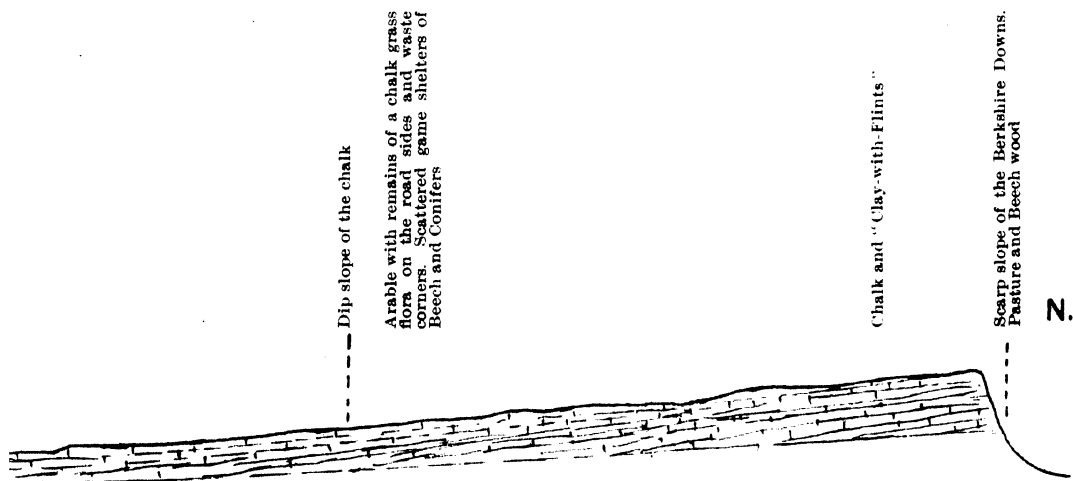
¹ *Types*, p. 76.

² *Ibid.* p. 205.

³ *Ibid.* p. 103.

⁴ *Ibid.* pp. 94, 109.

⁵ *Ibid.* p. 105; also Fritsch and Parker, *New Phytologist*, **12**, 1913, p. 149.



1borne Valleys from the Berkshire to the Wiltshire Downs.

surrounding heath from these plantations; (d) limited invasions of *Pteris* from neighbouring oak-birch woodland. The advance of the bracken was apparently purely vegetative, and seemed to occur only where *Calluna* was absent.

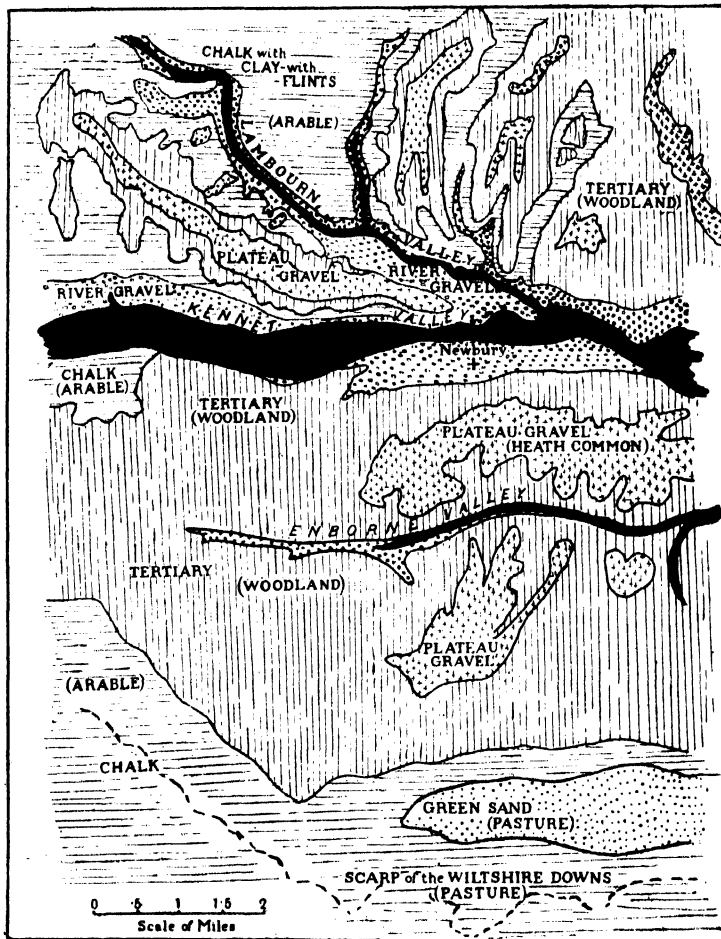


FIG. 2. Sketch-Map of the Newbury Region showing the relation of Geological structure with the Vegetation. Chalk, horizontal lines; Upper Greensand, dotted; Tertiary Sands and Clays, vertical lines; Plateau Gravel, crosses; River Gravel, circles; Alluvium, black.

Small streams form fairly deep valleys intersecting the heath area and cutting into the Tertiary beds. Alder swamps extend along these streams and give place to peat bogs at the heads of the valleys, with *Sphagnum* spp., *Myrica Gale*, *Narthecium ossifragum*, *Drosera* and *Eriophorum*, as constituents of the peat flora¹. Bordering the alder swamp is a narrow zone of *Juncus* (?) *effusus* which extends for some distance along the borders of the peat bog, and in places is bordered by a zone of *Molinia* which passes up into the pure

¹ *Types*, pp. 260, 263.

Calluna heath. Neither the *Juncus* nor the *Molinia* extends round the head of the bog, which abuts directly on *Callunetum*.

PRIMITIVE VEGETATION OF THE AREA.

The general conclusions as to the primitive vegetation of the area examined are as follows:

1. The alluvium of the Kennet valley was occupied by reed fen with a border of alder-willow carr.
2. The terraces of river gravel probably bore woodland of which there is no remaining trace.
3. The Tertiary sands and clays bore dry and damp oakwood respectively.
4. The Plateau Gravels capping the Tertiary ridges bore *Calluna* heath. The presence of well-grown pine remains in the peat at the heads of the stream valleys indicates the possibility that pinewood extended over the heads of these valleys and perhaps over the whole Plateau Gravel area.
5. The Chalk may have been entirely covered with grass or scrub or may have borne beechwood, the remains of which persist as game covers.
6. The Clay-with-Flints probably bore dry oakwood.

THE VEGETATION AS DETERMINING HUMAN ACTIVITIES.

1. The primitive settlements of herdsmen bordered the open chalk grassland, and gave rise to chains of villages such as Inkpen, West and East Woodhay, Highclere, Burghclere and Kingsclere. The woodland settlement of the hunter is now represented by the manor house of the sporting landowner (his lineal descendant), and its accompanying hamlet. Where the valley ways through the dry woodland of the river gravels approached one another on each side of a river at a ford, they gave easy access to the crossing and formed a nodal point which gave rise to ford settlements such as Newbury and Boxford.

2. The primitive roads and trackways kept to the lines of "good going" across dry open country, and mainly followed the edges of the chalk grassland (connecting the herdsmen's settlements) or the tops of the Tertiary ridges. Others led through the dry woods along the valley gravels bordering the river valleys.

3. The mediaeval buildings of timber and plaster are the results of the abundance of good oak in the neighbouring woodlands. The Cloth Hall at Newbury is a good example.

4. The obsolete woollen industry at Newbury was probably the result of the abundant natural sheep pasture on the neighbouring chalk, both on the dip-slopes and escarpments of the Downs. It would be interesting to enquire whether the destruction of the pastures by ploughing killed the industry, or whether the decay of the industry owing to competition led to the ploughing up of the pastures.

PRESENT-DAY LAND UTILISATION¹.

1. The drained and cleared valley bottoms are used for grazing (dairy and stock farms). The undrained land is under osiers for basket-making and the reed beds give thatching material and serve as cover for game.

2. The river terrace gravels, chalk dip-slopes and Clay-with-Flints are almost entirely arable grain-producing land.

3. The chalk escarpments and greensand inlier are mainly pasture.

4. The Tertiaries are mainly timber-producing, but where they have been cleared mixed farming is the rule.

5. The Plateau Gravels are almost entirely sterile waste land, but in some cases they have been planted with trees and produce timber.

TENDENCIES TO CHANGE IN LAND UTILISATION.

The following tendencies to change in the utilisation of the countryside were noted:

1. The planting of heathland to increase the yield of timber.

2. The response of a new section of the community (wealthy city workers who use the country as dormitory and pleasure ground) to the aesthetic appeal of the heathland and surrounding woods. This is resulting in the building up of purely residential settlements on the borders of the uninhabited heath.

¹ This was determined by a "transect" of the area, the use of the land on each side of the road, including every enclosure and the nature of the buildings, being noted on a six-inch map (1:10560). The general result was checked by means of a bird's-eye view from the top of Inkpen Beacon (1011 feet), the highest point in the area.

THE BRYOPHYTES AND LICHENS OF FRESH WATER

By W. WATSON.

A PROVISIONAL account of freshwater vegetation is given in *Types of British Vegetation*, and the main purpose of this paper is to give some further information in regard to the bryophytic flora. Freshwater habitats are very rich in bryophytes, especially where the water has a quick movement. The rocky beds of many mountain streams are covered with a prolific growth of mosses and liverworts, other plants, except minute algae, often being excluded. Though the mossy carpet usually consists of a mixture of bryophytic species, it often happens that one particular species becomes dominant. In a Pennine stream on Millstone Grit at Greenfield (Yorkshire) the rocky bed is thickly carpeted by a green form of *Alicularia compressa*, with occasional pure patches of *Scapania undulata* interrupting it. It seemed to be purely a matter of chance which was dominant on a particular part of the rocky bed, as both liverworts were growing under exactly similar conditions, and sometimes occurred mixed together. *Alicularia compressa* often occurs pure in mountain streams of Scotland and Wales but is usually of a redder colour, especially when the light intensity is high. *Scapania dentata* forms the main vegetation in some streams of siliceous districts, and in subalpine regions *S. uliginosa* and *S. obliqua* act similarly. In many streams from Kinder Scout (Derbyshire) *Aplozia riparia*¹ is abundant, whilst *A. cordifolia* often occurs in the subalpine regions of Wales and Scotland. Besides these, the chief liverworts which form pure masses are *Chiloscyphus polyanthus* and its varieties *fragilis* and *rivularis*², *Marsupella aquatica*, *Aneura sinuata*, *Eucalyx obovatus* and its variety *rivularis*, and *Madotheca porella*.

Amongst the Musci *Hypnum commutatum* or *Amblystegium filicinum* often forms a thick felting on the calcareous beds of streams, *Eurhynchium rusci-forme* is abundant over both siliceous and calcareous beds with a slight preference for the latter, and a slender lax-leaved form of *Bryum pseudotriquetrum* occurs in streams on Millstone Grit. In addition to the above, the principal mosses forming pure masses on the beds of streams are *Fontinalis antipyretica*, *F. squamosa*, *Brachythecium rivulare*, *Amblystegium irriguum*, *Hypnum riparium*, *H. falcatum*, *Hyocomium flagellare*, and *Philonotis fontana*. By the sandy sides of many streams of the Southern Pennines

¹ This is usually the form *potamophila* and has often been recorded as *A. cordifolia*.

² The variety *rivularis* occurs in swifter waters than the variety *fragilis*, though it is also met with in the pure water of some Highland lochs.

Catharinea crispa forms large tussocks and seems to be able to endure and adapt itself to the alkaline and turbid waters discharged from waste-cleaning factories.

In slowly moving waters bryophytes play a less important part, though their frequency is very variable, this variability being due to local circumstances and often directly traceable to human interference. *Hypnum riparium*, *H. cuspidatum*, *H. aduncum*, *Eurhynchium rusciforme*, and *Fontinalis antipyretica* are the most frequent and widely distributed, occurring in both siliceous and calcareous districts. The last three are sometimes given as preferring calcareous districts, but the preference is only a slight one. *Sphagna* are sometimes abundant but are very rarely, if ever, found in waters rich in mineral salts.

Few lichens are found completely submerged, though *Dermatocarpon aquaticum* and a few Verrucariae are common in some streams. *Verrucaria aquatilis* is a rather rare species of such a habitat, but I have often found *V. submersa* or its allied species (*V. aethiobola*, *V. laevata*, *V. margacea*, *V. hydrela*) completely covering the stones on the beds of streams as a greenish or dark incrustation dotted with the papilloid perithecia.

The treatment of the various freshwater habitats in which bryophytes occur follows the lines adopted in *Types of British Vegetation*.

I. THE SUB-FORMATION OF FOUL WATERS.

In these waters bryophytes are absent.

II. THE SUB-FORMATION OF SLOWLY-MOVING WATERS RELATIVELY RICH IN MINERAL SALTS.

(a) *Nearly stagnant waters.*

In waters containing phanerogams such as frog-bit and duckweeds the bryophytes are poorly represented. *Ricciocarpus natans* is usually found in such situations. The floating form has long, pendant, serrated, more or less violet scales on the ventral surface, and rhizoids are scarce or absent. The same plant may occur on the mud at the margins. In this terrestrial form the rosettes are less perfect, the colour is often darker and reddish, the rhizoids become abundant, and the ventral scales are greatly reduced, merely serving as a protection to the growing point. The ventral scales of the floating form not only serve as assimilating organs but also increase the surface so as to give a greater water-absorbing area and greater stability. In the terrestrial form the rhizoids are more efficient agents for obtaining a sufficient amount of dissolved substances and for ensuring stability.

Riccia fluitans is often associated with *Lemna*, and also has two forms, the terrestrial form having many rhizoids whilst the floating form has none. The terrestrial form may occur at the margins of the pools or may be completely submerged during wet periods, its rhizoids attaching it to the mud at the bottom of the water.

Hypnum aduncum, *H. cuspidatum*, *H. cordifolium* and *H. giganteum* sometimes occur in similar situations, but can scarcely be considered as members of this association.

(b) *Slowly flowing waters.*

(1) *Submerged.*

<i>Cinclidotus fontinaloides</i>	<i>H. riparium</i> var. <i>longifolium</i>	<i>H. aduncum</i>
<i>Fontinalis antipyretica</i>	<i>H. cuspidatum</i>	var. <i>paternum</i>
<i>Eurhynchium rusciforme</i>	<i>H. giganteum</i>	var. <i>intermedium</i>
<i>Hypnum cordifolium</i>		

(2) *On banks liable to frequent submergence.*

<i>Barbula tophacea</i>	<i>H. stellatum</i> var. <i>protensum</i>	<i>H. cuspidatum</i>
<i>B. cylindrica</i>	<i>H. aduncum</i>	<i>Amblystegium filicinum</i>
<i>Tortula mutica</i>	<i>H. commutatum</i>	<i>Pellia fabbroniana</i>
<i>Leskea polycarpa</i>	<i>H. polygamum</i>	<i>Aneura pinguis</i>
<i>Hypnum riparium</i>	<i>H. cordifolium</i>	<i>Lophozia turbinata</i>
<i>H. stellatum</i>	<i>H. giganteum</i>	

III. SUB-FORMATION OF SLOWLY-MOVING WATERS RELATIVELY POOR IN MINERAL SALTS.

(1) *Submerged.*

<i>Dicranella squarrosa</i>	<i>H. cuspidatum</i>	<i>Aneura pinguis</i> (long form)
<i>Webera albicans</i> var. <i>glacialis</i>	<i>Sphagnum cuspidatum</i>	<i>Pellia epiphylla</i>
<i>Splachnum vasculosum</i> (alpine)	var. <i>plumosum</i>	<i>Marsupella emarginata</i>
	var. <i>serratum</i>	<i>M. aquatica</i>
<i>Bryum pseudotriquetrum</i>	<i>S. torreyanum</i>	<i>Alicularia compressa</i>
<i>Mnium cinclidioides</i>	<i>S. rufescens</i>	<i>Gymnocolea inflata</i> form <i>nantensis</i>
<i>M. punctatum</i>	<i>S. crassicaudum</i>	<i>Cephalozia lammersiana</i>
<i>M. affine</i> var. <i>elatum</i>	<i>S. obesum</i>	<i>Chiloscyphus polyanthus</i> var. <i>riverialis</i>
<i>Fontinalis antipyretica</i>	<i>S. auriculatum</i>	<i>Scapania undulata</i>
<i>Eurhynchium rusciforme</i>	<i>S. cymbifolium</i> var. <i>squarrosum</i>	<i>Lepidozia setacea</i>
<i>Amblystegium irriguum</i>		
<i>Hypnum fluitans</i>	<i>Marchantia polymorpha</i> var. <i>aquatica</i>	
<i>H. exannulatum</i>		

(2) *On banks liable to frequent submergence.*

<i>Polytrichum commune</i>	<i>H. fluitans</i>	<i>Marsupella emarginata</i>
<i>P. strictum</i>	<i>H. cuspidatum</i>	<i>M. aquatica</i>
<i>Dicranella squarrosa</i>	<i>Sphagnum cymbifolium</i>	<i>Alicularia scalaris</i>
<i>Blindia acuta</i>	<i>S. imbricatum</i>	<i>Eucalyx obovatus</i>
<i>Fissidens adiantoides</i>	<i>S. papillosum</i>	<i>Aplozia riparia</i>
<i>Philonotis fontana</i>	<i>S. subnitens</i>	<i>Gymnocolea inflata</i> form <i>laxa</i>
<i>Aulacomnium palustre</i>	<i>S. inundatum</i>	<i>Chiloscyphus polyanthus</i> var. <i>fragilis</i>
<i>Bryum pseudotriquetrum</i>	<i>Conocephalum conicum</i>	<i>Cephalozia connivens</i>
<i>Eurhynchium rusciforme</i>	<i>Lunularia cruciata</i>	<i>C. bicuspidata</i>
<i>Hypnum riparium</i>	<i>Pellia epiphylla</i>	<i>C. fluitans</i>
<i>H. stellatum</i>	<i>Aneura pinguis</i>	<i>Calypogeia trichomanis</i>
<i>H. intermedium</i>	<i>A. multifida</i>	<i>Lepidozia setacea</i>
<i>H. exannulatum</i>	<i>A. major</i>	

IV. SUB-FORMATION OF QUICKLY FLOWING STREAMS.

In this sub-formation phanerogams are few, the vegetation largely consisting of bryophytes. Foliose liverworts are often very abundant.

Many of the bryophytes growing in the stream may also occur at the margins in places which are frequently submerged, or even where only occasionally submerged, since the splashes and spray caused by the water dashing against the stones may keep them constantly wet. Some species are more characteristic of one situation than of another and I have thought it advisable to arrange them under four groups of communities.

- (1) A community actually submerged in the stream.
- (2) A community growing in places where the plants are frequently submerged and are constantly kept moist through splashes or spray.
- (3) A community of less hydrophilous plants which are occasionally submerged and are often wet by splashes or spray.
- (4) A community of plants growing in or near waterfalls.

Each of these may again be arranged in regard to their occurrence in calcareous or non-calcareous waters. In the following lists this has not been done, but where a plant is distinctly a plant of non-calcareous waters S is prefixed, C similarly indicating a plant of calcareous waters. When the preference is less decided small letters (s and c) are used.

Many of the bryophytes given not only have no xerophytic devices but also show special hydrophytic characters. As a general rule the bryophytes of wet ground have larger cells than those of drier situations, the largest cells being shown by those bryophytes occupying a moist habitat (e.g. *Pterygophyllum lucens*). In some plants of rapid streams the cells are smaller than those of allied plants occurring on wet ground or in quieter waters, less strain being withstood by the latter (cf. *Chiloscyphus polyanthus* var. *rivularis* and var. *fragilis*, the cells of the former being little more than half the size of those of the latter). The cell-walls of the plants submerged in mobile waters are usually firmer or more thickened, this character again being connected with opposition to strain. Strong and numerous rhizoids which adhere firmly to the substratum are present. In plants of still waters or of wet ground the rhizoids are often fewer in number. In many plants (e.g. *Reboulia*) the form of wet ground has fewer rhizoids than the form of drier situations, as water is more easily obtainable by the general surface of the leaves or thalli.

The leaves of plants submerged in rapid streams or exposed to the splashes from waterfalls are often worn away on the lower parts of the stem, but some plants have devices protective against such injury. In some the leaves have a thickened border (e.g. *Cinclidotus*), in others the leaves are folded over (e.g. *Fontinalis*). Other devices such as papillation (e.g. *Dichodontium pellucidum*), recurving of the leaf-margin (e.g. *Bryum pseudotriquetrum*), and falcation of the leaf (e.g. *Hypnum commutatum*), though usually devices protective against loss of water, may prevent injury to the leaf. *Dicranella*

heteromalla when growing in or near mountain streams sometimes has its leaves very falcate, so that only the upper portions, consisting chiefly of the thickened midribs, are exposed, whilst the typical plant growing on damp soil possesses little falcation.

Reduction of many structures often occurs in plants of wet places; the pores may be reduced (e.g. *Marchantia*), the ventral scales may become fewer or disappear (e.g. *Dumortiera*), or the hyaline cells may be relatively less (e.g. *Sphagnum crassycladum*). In *Catharinea crispa* the assimilating lamellae are fewer and lower than in the allied species of drier ground and a similar reduction sometimes occurs in submerged Polytricha: in fact, a wet ground form of *P. gracile* with reduced lamellae was at first described as a new species (*Catharinea dixonii*) and placed in a genus characterised by its few lamellae. The strengthening fibres of the hyaline cells of *Sphagnum* may also be fewer, but such reduction does not occur in Sphagna living in rapid streams.

In rapid streams the plants are often very robust and much elongated (e.g. *Alicularia compressa*). Plants which are typically pinnate often lose their pinnate character, the branches becoming very long (e.g. *Eurhynchium rusciforme* var. *alopecuroides*). The leaves are often large and are sometimes lengthened. In *Pellia epiphylla* there are a number of strengthening bands and these are usually more pronounced in the form of rapid streams; in the plant of moist nooks (var. *efasciata*) they are fewer.

In some of the following lists the flowering plants have been added in order to give a better idea of the vegetation as a whole.

(1) *Submerged community.*

- | | |
|--|--|
| S. <i>Ranunculus lenormandi</i> f ¹ . | C. <i>obtusangula</i> , usually in still waters o. |
| R. <i>peltatus</i> o. | C. <i>stagnalis</i> l.a. |
| .. var. <i>penicillatus</i> f. | C. <i>intermedia</i> . All these species of <i>Callitriche</i> |
| R. <i>hederaceus</i> o. | are commoner in slowly moving waters. |
| C. R. <i>fluitans</i> f. | S. <i>Myriophyllum alterniflorum</i> l.a. |
| R. <i>circinatus</i> r. | C. <i>Enanthe crocata</i> o. |
| <i>Nasturtium officinale</i> , often small and dark | A. <i>apium nodiflorum</i> f. |
| in mountain streams o. | M. <i>myosotis palustris</i> o. |
| S. <i>Stellaria uliginosa</i> o. to l.a. | s. <i>Elodea canadensis</i> o. |
| S. <i>Montia fontana</i> , especially the var. <i>rivularis</i> l.a. | S. <i>Potamogeton pusillus</i> l.a. |
| S. <i>Peplis portula</i> o. | s. P. <i>crispus</i> l.a. |
| S. <i>Callitriche vernalis</i> o. | P. <i>polygonifolius</i> o. |
| | S. <i>Glyceria fluitans</i> l.a. |
| S. <i>Catharinea crispa</i> . On sand l.f. | F. <i>rufulus</i> . On stones r. |
| S. <i>Dichodontium flavescens</i> . On rock l.f. | S. <i>Rhacomitrium aciculare</i> . On rocks a. |
| S. <i>Dicranella squarrosa</i> . On sand or rock a. | c. <i>Cinclidotus fontinaloides</i> . On stones or |
| S. <i>Blindia acuta</i> . On rocks (commoner at | wood f. |
| sides) o. | C. <i>Orthotrichum rivulare</i> (usually a mar- |
| C. <i>Fissidens crassipes</i> . On stones o. | ginal plant) o. |

¹ The letters indicating the frequency are those usually employed. d. dominant, sd. sub-dominant, a. abundant, f. frequent, o. occasional, r. rare, vr. very rare, l. local.

- S. Aulacomnium palustre* (usually in boggy places) o.
- S. Philonotis fontana* a., *C. P. calcarea* o., and *S. P. caespitosa* o., are frequent in or near streams, though commoner in or near bogs.
- Webera ludwigii* var. *latifolia*. Alpine r.
- Bryum pseudotriquetrum*. A slender form is often abundant in streams on Millstone Grit o.
- B. bimum* (perhaps more frequent in calcareous districts) o.
- B. filiforme* and *B. concinnum*. On rocks r.
- B. alpinum* var. *distantifolium*. On stones vr.
- B. mildeanum* and *B. dixonii*. On rocks or sand r.
- Fontinalis antipyretica* (more frequent in slower streams, though its var. *gracilis* usually occurs in swift streams) lf.
- S. F. squamosa*. Often abundant in mountain streams f. to a.
- F. dalecarlica*, *F. dixonii* and *F. seriata* are rarer plants.
- c. *Leskea polycarpa* (commoner at the margins of quieter waters) o.
- Brachythecium rivulare*. Usually on stones a. Vars. *latifolium* and *catractarum* appear to be more frequent in siliceous districts r.
- c. *Aneura pinguis*. On rocks or soil f.
- s. *A. sinuata*. On stony bed. It is the most hydrophilous of the *Aneuras* f.
- S. Pellia epiphylla* and *C. P. fabbronia*. Commoner at the margins f. The var. *lorea* of the latter is usually submerged o.
- S. Marsupella marginata* (usually on rocks) f.
- S. M. aquatica*. Usually in more aquatic situations than the preceding and on rock l.f.
- M. sphacelata*. Alpine vr.
- S. Alicularia compressa*. On rocky or stony beds. Sometimes it becomes much elongated f. to sd.
- S. A. scalaris* vars. *distans* and *rivularis* r.
- S. Eucalyx obovatus* var. *rivularis*. Usually on rock r.
- S. Aplozia cordifolia*. On alpine or subalpine rocks l.a.
- S. Hyocomium flagellare*. On rocks a. In mountain streams it often becomes much elongated.
- Eurhynchium rusciforme*. On rocks or stony ground a. to sd. The lower portions are often dark and denuded of leaves.
- S. Amblystegium irriguum*. On stones, rarely in rapid streams f.
- c. *A. fluviatile*. On stones, often in rapid streams o.
- C. *A. filicinum* occasionally occurs on siliceous formations f. Var. *vallisclausae* o.
- Hypnum riparium*. On stones, wood, etc. f.
- H. fluitans* (usually in boggy places) o.
- S. H. exannulatum* especially var. *falcifolium* o.
- H. falcatum* (often a bog plant) o.
- C. var. *virescens* usually occurs in or near streams r.
- C. *H. commutatum* (rare on siliceous formations) a.
- S. H. stramineum* (often a bog plant) o.
- S. H. eugyrium*. On rocks o.
- S. H. ochraceum* and var. *flaccidum*. On rocks f.
- H. molle*, *H. dilatatum* and *H. arcticum* are alpine r.
- H. palustre* (usually on rocks) o.
- S. Sphagnum rufescens*, *S. auriculatum* and *S. obesum* o.
- S. S. crassycladum* f.
- A. riparia* form *potamophila* is often completely submerged lf. The var. *rivularis* is truly aquatic r.
- A. pumila* var. *rivularis* is a more aquatic plant than the type r.
- s. *Chiloscyphus polyanthus* is usually a marginal plant o. *S. var. rivularis* o. and var. *fragilis* f. are sometimes completely submerged.
- s. *Scapania dentata*. Often in marshy places a.
- S. S. undulata* is also common in marshy places a. to d.
- S. uliginosa* and *S. obliqua* are alpine or subalpine l.f.
- S. Madotheca porella* and *Jubula hutchinsiae*. On rocks r.

Lichens are few, though they may be locally abundant. They are attached to the rocky beds or on stones and are mostly crustaceous.

S. Collemodium fluviatile r.	Verrucaria submersa f.
Aspicilia lacustris r.	V. margacea r.
S. Lecidea semipallens r.	V. laevata o.
Dermatocarpon aquaticum f.	V. aquatilis r.
Polyblastia theleodes r.	V. aethiobola o.
P. subviridicans r.	

Algae are frequent, those given below being usually attached to stones in the bed of the stream.

C. Chara vulgaris and other species of Chara are usually plants of quiet waters.	S. S. fluviatilis o.
S. Nitella opaca usually found on the bot- tom of ponds.	S. fucina o.
S. Sacheria mammillosa f.	Lemanea torulosa o.
	L. parvula o.
	Chantransia spp. o.

Batrachospermum moniliforme and other species are occasionally submerged in streams but are often in quieter waters.

C. Rivularia haematites f.	Nostoc verrucosum f.
Lyngbya spp. o.	N. sphaericum f.
Oscillatoria irrigua (dark purplish patches) f.	Ulothrix zonata is not uncommon on stones in streams.
O. muscorum and other species o.	Stigeoclonium tenue and other species o.

Draparnaldia glomerata is usually found in quiet waters; when present in rapid streams it only occurs where the stream is impeded.

Cladophora glomerata a.	s. Choaspis stictina o.
Hydrurus foetidus r.	Spirogyra insignis o.

Other species of *Spirogyra* usually found in quiet waters are occasionally present.

Vaucheria usually occurs in quiet waters but *V. sessilis* is sometimes found in rapid streams.

(2) *Frequently submerged and kept moist by splashes or spray.*

Phanerogams are more conspicuous but the main vegetation often consists of bryophytes.

S. Ranunculus lenormandi o.	Apium nodiflorum f.
R. hederaceus o.	Œnanthe crocata o.
R. flammula l.a.	Veronica beccabunga f.
R. peltatus o.	S. Sibthorpia europaea l.f.
Nasturtium officinale a.	S. Mimulus langsдорffii and M. moschatus on stones l.f.
S. Stellaria uliginosa l.a.	Myosotis palustris a.
Sagina nodosa o.	Alopecurus geniculatus f.
s. Chrysosplenium oppositifolium l.a.	Lycopodium inundatum r.
c. C. alternifolium o.	Selaginella selaginoides r.
S. Montia fontana l.a.	
S. var. rivularis l.a.	

- S. Catharinea crispa*. Among sand or grass l.f.
- S. Polytrichum commune* is rather a plant of marshy places a.
- S. Dichodontium pellucidum*. Usually on rock a.
- S. D. flavescens* is often submerged o.
- S. Dicranella schreberi* var. *elata* o.
- S. D. squarrosa*. Usually on sandy bed a.
- S. Blindia acuta*. On rock, sometimes on soilcap l.a.
- S. Fissidens osmundoides*. On rock o.
- S. F. adiantoides* (often a bog plant). On rock o.
- C. F. crassipes*. On rock o.
- C. F. decipiens*. On rock or grassy bank o.
- Grimmia apocarpa* (usually on drier rocks) o. Its varieties *rivularis*, *gracilis* and *alpicola* are often found on boulders of the stream l.f.
- S. Rhacomitrium aciculare*. On rocks f.
- S. R. ellipticum*. On rocks r.
- Barbula spadicea*. On rocks or sand o.
- C. B. tophacea*. Usually on wet rock o.
- C. Weisia rupestris* and *W. verticillata* on rock o.
- S. Trichostomum tenuirostre* and var. *holtii*. On rocks o.
- S. Zygodon mougeotii*. On rocks f
- C. Orthotrichum rivulare*. On rocks and tree roots o.
- S. Philonotis fontana* and *P. caespitosa* on sandy or peaty sides f.
- C. P. calcarea* (often in bogs). On wet ground o.
- Conocephalum conicum*. Usually on rock just above the water a.
- Lunularia cruciata* is rather a plant of damp places o.
- Dumortiera hirsuta*. On dripping rocks o.
- c. *Preissia quadrata* (usually on rocks) o.
- s. *Marchantia polymorpha*. Often on boulders in stream o.
- Aneura pinguis*. Often present amongst wet rocks or soil f.
- s. *A. multifida*. Wet rocks and soil f.
- S. Pellia epiphylla*. Wet rocks and soil a.
- S. P. neesiana*. On grassy ground, or on rocks o.
- Bryum pseudotriquetrum* and *B. bimum* on wet ground or rocks a.
- Mnium punctatum*. On ground, rocks or soilcaps a.
- s. *Pterygophyllum lucens*. On ground or stones f. to a.
- C. Porotrichum angustifolium* r.
- P. alopecurum*. On ground, rocks or soilcaps a. to sd.
- Brachythecium rivulare* and *B. plumosum*. Usually on rocks f.
- S. Hyocomium flagellare*. Usually on rock a.
- Eurhynchium rusciforme*. Usually on rock a.
- S. E. myosuroides* var. *rivulare*. On rock r.
- C. E. teesdalei* and *E. curvisetum* o.
- S. Sematophyllum micans* and var. *badense*. On rocks r.
- S. Amblystegium irriguum*. On stones o.
- C. A. filicinum* and var. *trichodes* f.
- Hypnum riparium*. On stones, ground, etc. a.
- S. H. exannulatum*, *H. revolvens*, and *H. intermedium* o.
- C. H. commutatum*. On rock or soil f.
- C. H. molluscum* (usually drier places). On rock or soil o.
- H. palustre*, *H. eugyrium* and *H. ochraceum* o.
- S. Sphagnum molle*, *S. squarrosum*, *S. subnitens* o.
- S. S. cymbifolium* especially its var. *squarrosum* o.
- S. S. rufescens*, *S. inundatum*, *S. auriculatum* f.
- C. P. fabbronia*. On rocks or on ground a.
- S. Marsupella emarginata* and *M. aquatica* (usually on rock) f.
- S. Alicularia scalaris* (usually drier situations) and var. *procerior*. On ground or rock o.
- S. Eucalyx obovatus* especially forms *elongatus* and *laxus*. On rocks or soil f.
- S. Aplozia sphaerocarpa*. On rock or soil f.
- S. A. cordifolia*. More frequently a submerged plant o.
- A. riparia* especially form *potamophila* f.
- A. atrovirens*. In wet rocky places r.
- A. pumila*. On rocks or in gravelly places o.

- S. Gymnocolea inflata* (usually on peaty sides) o.
c. Lophozia muelleri. On alpine and sub-alpine rocks l.f.
s. L. bantriensis. On alpine and subalpine rocks and ground o.
L. kunzeana on wet ground. Alpine vr.
s. Sphenolobus politus. Wet ground. Not uncommon in alpine regions and is usually associated with *Harpanthus flotowianus* and *Lophozia bantriensis* r. to lf.
Chiloscyphus polyanthus. Wet ground a.
s. var. *fragilis*. Often on rocks just above the level of the stream a.
s. Harpanthus flotowianus. Sides of streams. Alpine l.
Cephalozia bicuspidata. Sides of streams a.
Calypogeia fissa. On ground, usually when peaty f.
Blepharostoma trichophyllum. On ground, rocks or stumps o.
Trichocolea tomentella. On ground o.
s. Diplophyllum albicans (longer and more robust form) f.
S. Scapania subalpina. Subalpine, on gravelly detritus r.
S. nemorosa var. *uliginosa*. Usually in marshes o.
S. dentata. On wet rocks or soil a.
S. Jubula hutchinsiae. Rocks or caves o.
Anthoceros laevis (form). On ground r.

Lichens are not abundant: they chiefly belong to the crustaceous group, and are usually attached to rocks.

- Collemodium fluviatile* r.
Spilonema paradoxum o.
Pilophorus cereolus r.
Aspicilia lacustris r.
A. epulotica r.
S. Lecidea contigua form *hydrophila* a.
Bacidia inundata o.
Rhizocarpon perlutum vr.
R. obscuratum var. *lavatum* r.
Dermatocarpon miniatum var. *complicatum* f.
Polyblastia theleodes r.
Porina lectissima r.
Verrucaria hydrela r.
V. margacea o.
V. papillosa o.

Many algae occur on the wet rocks or on the bryophytes which are frequently submerged. The following list gives some of the characteristic algae found.

- Batrachospermum* spp. and *Chantransia* spp. o.
C. Rivularia haematites f.
Dichothrix orsiniana f.
Stigonema spp. f.
Rivularia crustacea o.
C. Scytonema myochrous (in felt-like masses) f.
C. S. alatum forms a brownish-green stratum f.
C. Schizothrix calcicola and *S. lardacea* o.
Plectonema tomasinianum in brownish felt-like masses.
C. Phormidium purpurascens in purplish masses.
Nostoc muscorum and *N. humifusum* f.
N. commune (wet ground) f.
Species of *Oscillatoria*, *Gloeocapsa* and *Lyngbya* f.

Many Chlorophyceae, especially the unicellular members, are present.

(3) Occasionally submerged.

Phanerogams become more abundant, but bryophytes are still dominant. Most of the plants given as occurring in (2) also occur in this association and may be supplemented by many others.

<i>Thaliotrum minus</i>	<i>Oxyria digyna</i>	<i>C. oederi</i>
<i>Stellaria media</i>	<i>Polygonum viviparum</i> (alpine)	<i>C. pulicaris</i>
<i>Cardamine amara</i>	<i>Tofieldia palustris</i> (alpine)	<i>Equisetum palustre</i>
<i>Hypericum tetrapterum</i>	<i>Narthecium ossifragum</i>	<i>E. hyemale</i>
<i>Oxalis acetosella</i>	<i>Juncus articulatus</i>	<i>E. variegatum</i>
<i>Lotus uliginosus</i>	<i>J. bulbosus</i>	<i>Phyllitis scolopendrium</i>
<i>Geum rivale</i>	<i>J. triglumis</i> (alpine)	<i>Polystichum aculeatum</i>
<i>Saxifraga hypnoides</i>	<i>J. biglumis</i> (alpine)	<i>Lastrea filix-mas</i>
<i>Epilobium tetragonum</i>	<i>Luzula maxima</i>	<i>L. montana</i>
<i>Wahlenbergia hederacea</i>	<i>L. pilosa</i>	<i>Hymenophyllum tunbridgense</i>
<i>Lysimachia nemorum</i>	<i>Scirpus setaceus</i>	<i>H. peltatum</i>
<i>Mentha aquatica</i>	<i>Carex echinata</i>	
<i>S. Andreaea petrophila</i> o.	<i>C. Barbula cylindrica</i> a.	<i>W. albicans</i> a.
<i>S. Tetraphis browniana</i> l.	<i>B. fallax</i> a.	<i>Bryum pallens</i> f.
<i>Swartzia montana</i> l.f.	<i>Weisia curvirostris</i> r.	<i>B. capillare</i> var. <i>flaccidum</i> o.
<i>s. Ceratodon purpureus</i> o.	<i>S. Anocetangium compactum</i>	<i>S. Heterocladium heteropterum</i> f.
<i>S. Cynodontium polycarpum</i> o.	var. <i>pellucidum</i> r.	<i>Thuidium tamariscinum</i> a.
<i>S. Dicranella crispa</i> o.	<i>C. Cinclidotus brebissoni</i> o.	<i>C. T. philiberti</i> o.
<i>S. D. heteromalla</i> o.	<i>S. Discelium nudum</i> r.	<i>Amblystegium serpens</i> f.
<i>D. rufescens</i> o.	<i>S. Funaria templetoni</i> o.	<i>S. Sphagnum quinquefarium</i> l.a.
<i>D. varia</i> o.	<i>S. Breutelia arcuata</i> l.f.	
<i>D. schreberi</i> o.	<i>Webera carnea</i> f.	
<i>C. Reboulia hemisphaerica</i> (often drier places) o.	<i>Hygrobiella laxifolia</i> (subalpine) r.	<i>Madotheca rivularis</i> o.
<i>Metzgeria conjugata</i> o.	<i>Eremonotus myriocarpus</i> (subalpine) r.	<i>S. Colurolejeunea calyptrifolia</i> r.
<i>S. Eucalyx hyalinus</i> o.	<i>S. Calypogeia trichomanis</i> o.	<i>C. Cololejeunea calcarea</i> o.
<i>c. Lophozia turbinata</i> f.	<i>S. Lepidozia trichoclados</i> o.	<i>C. C. rosettiana</i> o.
<i>c. L. badensis</i> f.	<i>s. Scapania intermedia</i> o.	<i>Lejeunea cavifolia</i> f.
<i>s. Plagiochila spinulosa</i> o.	<i>s. S. irrigua</i> o.	<i>L. patens</i> f.
<i>s. P. punctata</i> o.	<i>s. S. umbrosa</i> o.	<i>s. Harpalejeunea ovata</i> o.
<i>s. P. tridenticulata</i> o.	<i>Radula aquilegia</i> r.	<i>Drepanolejeunea hamatifolia</i> o.
<i>s. Lophocolea bidentata</i> form <i>latifolia</i> o.	<i>R. voluta</i> r.	<i>Frullania tamarisci</i> f.

The lichens are chiefly represented by crustaceous forms but a few foliaceous and fruticulose species are occasionally present.

<i>Ephebe pubescens</i>	<i>S. fuliginosa</i>	<i>Coenogonium ebeneum</i>
<i>Collema flaccidum</i>	<i>Peltidea aphthosa</i>	<i>Racodium rupestre</i>
<i>C. pulposum</i>	<i>Peltigera rufescens</i> var. <i>prae-textata</i>	<i>Lecidea contigua</i>
<i>C. C. multipartitum</i>	<i>Parmelia laevigata</i>	<i>Dermatocarpon lachneum</i>
<i>C. C. furvum</i>	<i>Lecanora coilocarpa</i>	<i>D. hepaticum</i>
<i>Stictina sylvatica</i>		

Algae are less abundant, being chiefly represented by unicellular species occurring amongst the wet bryophytes.

The list of bryophytes given above could be extended since a stream side is a particularly good habitat for both mosses and liverworts. It is one of the most favourable for the majority of mosses, and is the only one below sub-

alpine regions in which we meet with both abundance and diversity of liverworts.

Many of the species of this association flourish more freely in well-shaded ravines, dells, etc., where the conditions are always humid. This is especially true of the following species: *Porotrichum alopecurum*, *Heterocladium heteropterum*, *Bryum capillare* var. *flaccidum*, *Mnium punctatum*, *Plagiöchila spinulosa*, *P. punctata* (W), *P. tridenticulata* (W), *Metzgeria conjugata*, *Blepharostoma trichophyllum*, *Trichocolea tomentella*, *Scapania umbrosa*, *Radula aquilegia* (W), *R. voluta* (W), *Madotheca rivularis*, *Colurclejeunea calyptrifolia*, *Cololejeunea calcarea*, *Lejeunea patens*, *Harpalejeunea ovata* (W), *Drepanolejeunea hamatifolia* (W). Some of these, which are indicated in the text by W, are usually confined to the more humid ravines of the west.

The vegetation of these well-shaded ravines is sufficiently distinct to rank as a sub-association or even as a separate association. Nantcol Glen near Harlech in N. Wales, Clifton gully near Tyndrum in Perthshire and Holford Combe (upper reaches) in Somerset may be given as presenting different facies. They all agree in having a deep gully with a constant flow of water at the bottom and the sides overhung with trees. The altitude is nearly the same, though the Tyndrum stream (800 ft.) is somewhat higher and owing to its latitude and situation is much more subalpine in character than the other two, the Somerset gully showing no subalpine indications in its vegetation. Both the Tyndrum and Nantcol streams have rocky beds with many rocky shelves on the sides and boulders scattered on the base or piled up on the sides, whilst the Somerset stream is much less rocky and its floristic composition consequently less diverse. The rocky substratum in all three cases is chiefly siliceous though the Clifton burn possesses some schistose rocks with lime contents, *Hypnum molluscum* and some other calcicole species being present. The trees shading the gullies are chiefly birch at Tyndrum and oak at Nantcol and Holford Combe.

The following list gives the characteristic bryophytes. The frequency of the species is indicated by the usual abbreviations; when a dash is employed it merely indicates the presence of the plant without giving any information as to its frequency. The abbreviation abs signifies the probable absence of the species, whilst c.fr. is added in some cases to indicate that sporogonia have been found on plants which are rarely fertile.

	<i>Tyndrum</i>	<i>Nantcol</i>	<i>Holford Combe</i>
Soil	Subalpine	Slightly subalpine	Upland
Shaded chiefly by	Somewhat calcareous	Siliceous	Siliceous
Rocky character	Birch	Oak	Oak
	Strong	Strong	Weak
<i>Tetraphis pellucida</i>	o	r	f
<i>Catharinea undulata</i>	o	f	f
<i>Polytrichum aloides</i>	o	f	f

	<i>Tyndrum</i>	<i>Nantcol</i>	<i>Holford Combe</i>
<i>P. formosum</i>	—	o	f
<i>Dichodontium pellucidum</i>	a	a	a
<i>Fissidens adiantoides</i>	a	o	o
<i>F. bryoides</i>	o	o	o
<i>F. osmundoides</i>	o	—	abs
<i>Grimmia hartmani</i> and <i>G. retracta</i>	—	r	abs
<i>Rhacomitrium aciculare</i>	o	f	f
<i>R. protensum</i>	—	f	abs
<i>Barbula cylindrica</i>	a	o	r
<i>B. fallax</i>	o	o	o
<i>Breutelia arcuata</i>	o	o	r
<i>Weisia curvirostris</i>	o	r	abs
<i>Bryum capillare</i>	f	a	a
<i>Mnium hornum</i>	f	f	a
<i>M. undulatum</i>	o	o	a
<i>M. punctatum</i>	f	a	a
<i>Pterygophyllum lucens</i>	f	o	a
<i>Porotrichum alopecurum</i>	a	a	a
<i>Heterocladium heteropterum</i>	o	a (c. fr.)	a
<i>Pterogonium gracile</i>	r	o	abs
<i>Orthothecium rufescens</i>	f	abs	abs
<i>Thuidium tamariscinum</i>	o	a	f
<i>T. delicatulum</i>	—	f	abs
<i>Eurhynchium praelongum</i>	f	f	f
<i>var. stokesii</i>	—	o	r
<i>E. myosuroides</i>	f	a	a
<i>var. rivulare</i>	—	o	abs
<i>E. rusciforme</i>	f	a	a
<i>Hypnum molluscum</i>	a	r	r
<i>H. cupressiforme</i>	a	a	a
<i>H. cuspidatum</i>	o	a	a
<i>Sematophyllum micans var. badense</i>	abs	r	abs
<i>Hyocomium flagellare</i>	r	a	o
<i>Plagiothecium undulatum</i>	f	a	a
<i>P. denticulatum</i>	o	f	f
<i>P. elegans</i>	o	a (c. fr.)	f
<i>Brachythecium plumosum</i>	—	a	o
<i>Preissia quadrata</i>	f	abs	abs
<i>Aneura pinguis</i> (drawn form)	a	r	r
<i>Metzgeria conjugata</i>	a	f	o
<i>M. hamata</i>	—	r	abs
<i>Pellia epiphylla</i>	f	a	a
<i>Marsupella emarginata</i>	o	f	r
<i>Eucalyx obovatus</i>	o	f	abs
<i>Aplozia riparia</i>	o	—	o
<i>A. pumila</i>	f	—	r
<i>A. atrovirens</i>	o	abs	abs
<i>Lophozia muelleri</i>	a	abs	abs
<i>Plagiochila spinulosa</i>	f	f	f
<i>P. punctata</i>	—	f	abs
<i>P. tridenticulata</i>	abs	r	abs
<i>P. asplenoides</i>	o	f	a
<i>Lophocolea cuspidata</i>	o	o	f
<i>L. bidentata</i>	o	o	a
<i>Saccogyna viticulosa</i>	—	a	r
<i>Chiloscyphus polyanthus</i>	o	o	o
<i>Cephalozia bicuspidata</i>	f	f	a
<i>Blepharostoma trichophyllum</i>	a	f	abs
<i>Trichocolea tomentella</i>	o	o	o
<i>Diplophyllum albicans</i>	o	a	a
<i>Scapania gracilis</i>	—	a	r
<i>S. nemorosa</i>	o	o	r
<i>S. undulata</i>	o	a	a
<i>S. dentata</i>	o	a	a
<i>Radula lindbergii</i>	—	r	abs
<i>R. aquilegia</i>	abs	r	abs
<i>R. voluta</i>	abs	r	abs

	<i>Tyndrum</i>	<i>Nantcol</i>	<i>Holford Combe</i>
<i>Colurolejeunea calyptrifolia</i>	abs	r	abs
<i>Lejeunea cavifolia</i>	a	a	a
<i>L. patens</i>	a	a	abs
<i>Drepanolejeunea hamatifolia</i>	abs	a	abs
<i>Harpalejeunea ovata</i>	abs	a	abs
<i>Frullania tamarisci</i>	o	a	o
<i>F. fragilifolia</i>	—	f	abs
<i>Hygrobiella laxifolia</i>	f	r	abs
<i>Adelanthus decipiens</i>	abs	r	abs
<i>Calypogeia fissa</i>	a	f	o
<i>C. trichomanis</i>	o	a	f
<i>Jubula hutchinsiae</i>	abs	r	abs
<i>Madotheca porella</i>	abs	r	abs

(4) *Waterfalls.*

Many bryophytes are characteristic of this habitat; lichens are rarely present but some algae are common. Some of the characters shown by the bryophytic members of this association are given on page 74.

<i>Tetraphis browniana</i> o.	<i>S. Trichostomum tenuirostre</i>	<i>Heterocladium heteropterum</i>
<i>S. Blindia acuta</i> l.a.	var. <i>holtii</i> o.	f.
var. <i>trichodes</i> r.	<i>C. Orthotrichum rivulare</i> f.	<i>s. Porotrichum alopecurum</i> a.
<i>S. Dichodontium pellucidum</i>	<i>S. Philonotis fontana</i> o.	<i>Brachythecium rivulare</i> f.
a.	<i>S. P. caespitosa</i> o.	var. <i>cataractarum</i> o.
<i>S. D. flavescens</i> o.	<i>C. P. calcarea</i> o.	<i>Eurhynchium rusciforme</i> a.
<i>S. Rhacomitrium aciculare</i> a.	<i>S. Breutelina arcuata</i> f.	<i>S. Hyocomium flagellare</i> f.
<i>S. R. ellipticum</i> r.	<i>Bryum pallens</i> o.	<i>Sematophyllum micans</i> r.
<i>Fissidens rivularis</i> r.	<i>B. pseudotriquetrum</i> o.	<i>S. Hypnum ochraceum</i> o.
<i>C. Weisia verticillata</i> f.		<i>S. var. flaccidum</i> f.
<i>Conocephalum conicum</i> f.	<i>C. P. fabbroniana</i> var. <i>lorca</i> o.	<i>Aplozia pumila</i> f.
<i>S. Pellia epiphylla</i> (often elongated) f.	<i>S. Marsupella emarginata</i> o.	<i>Plagiochila spinulosa</i> o.
	<i>Lejeunea holtii</i> l.	<i>Jubula hutchinsiae</i> o.
<i>S. Ephebe pubescens</i> o.	<i>S. Lecidea contigua</i> form <i>hydrophila</i> o.	
<i>Chantransia chalybea</i> o.	<i>Rivularia crustacea</i> o.	<i>Cladophora glomerata</i> f.
<i>Batrachospermum</i> spp. o.	<i>Phormidium purpurascens</i> o.	<i>Vaucheria sessilis</i> (form) f.
<i>Stigonema</i> spp. o.	<i>Stichococcus variabilis</i> o.	

I am much indebted to many botanical friends (especially Mr D. A. Jones) for pleasant and helpful comradeship in my field-work, and also to Messrs Dixon, Macvicar, Nicholson and Wheldon for testing many critical bryophytes and for help in other ways.

REVIEW

Bews, J. W. *The Grasses and Grasslands of South Africa*. Pietermaritzburg (Davis & Sons, Ltd.), 1918, pp. 161, 24 figs. and 1 map. 7s. 6d.

The need for books of reference on the crop plants of the various parts of the British Empire is obvious. The systematic "Flora" is generally forthcoming, but this as a rule fails to convey the relative economic value of the species, and it rarely presents any picture of the relation to environment. Grasses are a formidable group because they require consideration from many points of view—taxonomic, morphological, ecological and economic. Few of the many books have done the grasses justice. The herbarium specimen and the laboratory transverse section are too obvious in the more exact books, while the more popular are generally superficial. The living grass, its mode of life, habitat and economic value does not seem to be easy to express. *The Grasses and Grasslands of South Africa* is in the first place ecological, and its perusal leaves a more satisfied feeling. It is one of a series of contributions by the author, which began with a general account of the vegetation of Natal (1912), and each year has seen some addition which either extended the area under survey, or dealt more intensively with some plant formation. When the time came for a more detailed treatment of grasslands, the material required more than a Society's Transactions, and this book is the result.

South Africa has over 500 grasses, almost all unfamiliar in the north temperate countries. The preliminary part of the book is therefore a taxonomic key (40 pp.). This is based on floral characters and it is workable so far as one can judge from familiar species. Simplicity is promoted by carrying the analysis in the first instance to the genus only; a set of supplementary keys is provided for the remaining species. How much the genera differ from European ones is seen at a glance: *Andropogon* (32 species), *Aristida* (24), *Eragrostis* (45), *Panicum* (38), *Pentstemon* (38), etc. Ordinary European grasses play a very minor part, the majority being colonists. To become acquainted with this large and unfamiliar flora, is in itself no small task for the author, who went from Britain to his present post about fifteen years ago.

The third section of the book (37 pp.) consists of ecological notes on the principal species, "to set forth the principal facts that have been ascertained, regarding the part played by all the more important species in the grassland plant succession, and also by means of selected examples, to illustrate the general differences which are shown in morphological characters, and particularly in leaf anatomy." In estimating the value of a grass as herbage, emphasis is laid on leaf structure. Thus a grass which is forced to protect itself against excessive transpiration must be hampered in photosynthesis, hence xerophytic grasses, with some exceptions, grow slowly and are less valuable pasturage than mesophytic grasses. Again, xerophytic grasses have generally a high proportion of sclerenchyma, hence they are avoided by stock. The more important grasses are illustrated by about twenty figures of leaf anatomy. The ecological notes are informative though brief, so that one sees at a glance that *Anthistiria imberbis* is the most important grass in South Africa, whereas Marram grass is planted only. Information is also given whether the grass is a coloniser in the early stages of a succession, or a constituent of one of the later stages.

These preliminary sections prepare the way for the main thesis—"A general sketch of

the Grasslands of South Africa and their development" (50 pp.). The nomenclature used is that of F. E. Clements in "Plant Succession," reviewed in this JOURNAL (4, pp. 198-204, 1916). Five grassland regions are recognised and indicated on a map: the Cape region passes northwards into the Karroid Central region, and this again into the Sand Veld or Kalahari region; the remaining two regions are broad zones following the western and eastern coasts¹.

South-western or Cape region of Fynbosch (Macchia). This is the region of Marloth's "Das Kapland," with extensions eastwards at higher altitudes. The winter rainfall and dry summers are unfavourable to grassland, though 200 species of grasses are recorded. The lithosere is extensive, and is followed by the xerosere with mosses and isolated flowering plants. Accumulation of soil is accompanied by a Macchia with hundreds of species of sclerophyllous shrubs. The grasses are temperate in type, with the Aveneae conspicuous and including *Danthonia*, *Achneria*, *Pentaschistis*, etc.; a large proportion are endemic. The hydrosere is related to springs and stream banks, habitats favourable to grassland in northern temperate countries, but here in the Cape region too unstable and liable to drought to favour grassland. The psammosere of the extensive coastal dunes is colonised mainly by *Sporobolus pungens* or by *Eragrostis* spp. The general succession everywhere is towards a Macchia of sclerophyllous shrubs. Numerous ruderal grasses, etc., mark the initial stages of a sub-sere, which is naturally replaced by Macchia, but under the influence of man—burning, stock-grazing, etc.—this may become relatively stable, as on ostrich farms.

The Western region extends from the Namib northwards towards Damaraland, and is largely unexplored. It begins in the south-west with initial stages of the desert which rarely attain to grassland, but northwards it passes into a moister and tropical climate where grassland increases.

The Sand Veld of the Kalahari and Central region. This is the third region of the central series, Cape, Karroo, Sand Veld. It extends from the Orange River to Bechuanaland, and abuts on the eastern region about Kimberley. The dominant feature is sand or fixed sand dunes with no surface water, because the ten to twelve inches of rainfall passes quickly into an underground drainage. *Aristida* Veld characterises the south-western drier parts, but with increasing rainfall eastwards there is a transition to the High Veld grassland of the Transvaal and Natal. The Sand Veld links up the Western, Karroo, and Eastern regions. It presents a contrast to the Cape region because the grass tribes are tropical and sub-tropical Paniceae, Stipeae, Andropogoneae, etc. The Grass Veld in many places proceeds to Tree Veld with Acacias, etc.

The Karroo and Karroid Central region. This lies central to the other four regions, and marginally it grades into them. The climate is continental and dry (3-14 in. rainfall). The dominant vegetation is a succulent and sclerophyllous dwarf shrub type, made up of Crassulaceae, Aizoaceae, and Compositae. There is no definite grassland type, except such as follows streams and depressions, and this is subject to considerable fluctuation, increasing with rainfall and decreasing with drought. Between the Karroo and the Eastern Grass Veld there is a transitional belt where Karroo and Composite Veld occur as patches interspersed with grassland. The Karroo vegetation follows soils with the surface dry and hardened, and this condition is extending eastwards because through overstocking the grasses are eaten out, and the stock-tracks tend to become dongas which encourage the run-off of water and thus promote a baked surface. The succession on this xerosere shows three stages which may be taken as typical. In the early stages Kweek-grass (*Cynodon incompletus*) is one of the more widespread consocieties which often forms a prostrate turf, useful for grazing. This is followed by an associates distinguished by *Aristida*—*Eragrostis*—

¹ Cf. Bews, J. W. "The chief Types of Vegetation in South Africa," this JOURNAL, 4, pp. 129-159, 1916.

Sporobolus, which passes under suitable conditions into a climax stage, the *Anthistiria-Andropogon* Veld, one of the characteristic types of the Eastern Grassland region. Better grazing is obtained from the *Anthistiria* or Red-grass, than from the *Aristida* type, but the farmers by burning and overstocking destroy the former, and throw the succession back to the earlier and less useful stage. Another succession has its climax in "Haas-gras" Veld (*Danthonia purpurea*). There is evidence that this has replaced the Red-grass veld as a result of the white settlers and their stock.

The Eastern Grassveld region. This, the chief grassland region of South Africa, includes most of the Orange Free State, Transvaal and Natal. It is a climatic formation distinguished by summer rainfall and a dry period coinciding with the season of lower temperatures. Within this greater formation there are well-marked and extensive divisions, even in the grasslands. Two main factors operate to bring about differentiation: the distribution of the rainfall, and the rapidly increasing altitude from the coast to the mountains culminating in the Drakensberg. The chief features of the region have already been described by Bews, and reviews of them in this JOURNAL may be consulted¹. The rain-bearing winds come from the Indian Ocean, and deposition takes place so that the slopes and terraces (High Veld) receive more than the valleys of the river systems (Low Veld). These two types of grassland—High and Low Veld—make up most of the area. A coastal grassland from Durban northwards has more tropical conditions, while beyond the Veld formations a tussock grassland is developed at higher altitudes on the Drakensberg, etc. The author has evidently found the same complexity in delimiting grasslands as is met with in other grassland countries. The present book affords an opportunity of testing the value of the successional mode of study, and the results are distinctly helpful. Thus we have separate studies on the succession in the xerosere, the hydrosere, and the psammosere. The xerosere begins with initial stages: lichen colonies, Cyanophyceae, Mosses and Hepatics, *Selaginella*, etc. The initial grassland consists of pioneer grasses; chiefly species which are xerophytic, deep-rooted, and light-demanding, e.g. *Aristida* spp. There is thus a similarity between the initial stages of the Eastern grassland, and the climax stages in the Western and Karroo regions, as already indicated. *Aristida-Eragrostis-Sporobolus* and *Cynodon* or Kweek-grass, are prominent genera in these initial stages. The climax stages of stable grassland begin when grasses, mostly *Andropogoneae* (e.g. *Anthistiria imberbis*) appear. These are less xerophytic and form mats which protect the surface of the soil and at the same time suppress the pioneers. The climax stages include many plant societies and clans, including *Compositae*, *Leguminosae*, etc., which distinguish and add considerably to the vernal aspects that accompany the first rains.

The Grassveld is a widespread climax stage, but there is evidence that on parts of the High Veld, the succession will go on to forest or post-climax grassland. The first stage is replacement of *Andropogon-Anthistiria* Veld by taller species of *Andropogon*, etc. ("Tambookie"). In the transition to forest, these give place to shrubs or other flowering plants, in places to *Pteris aquilina*. The forest phase includes *Podocarpus* (yellow-wood), *Leucosidea*, or it may be Bush Veld or Thorn Scrub. From the stock-grazing outlook this transition to Tambookie or Bush is not advantageous, and the succession is prevented by burning the coarser grasses, thus maintaining the *Anthistiria* stage.

Economic applications are dealt with in a special section, which contains the nucleus of an important branch of Agrostology. One important thesis is that the effect of grass-burning depends on the type of grassland, and on the stage at which the plant succession has arrived. If the grass veld is primitive or semi-open, burning prevents the succession from proceeding further: thus a less useful grassland (e.g. *Aristida-Eragrostis-Sporo-*

¹ (a) "The Vegetation of Natal" (1912), this JOURNAL, **1**, p. 75.

(b) "An Ecological Survey of the Midlands of Natal" (1913), *idem* **2**, p. 206.

bolus) may be prevented from becoming a better type, although for the current year burning may improve the edible qualities of the grasses. If the grass veld has proceeded further towards a more stable type (*Anthistiria* stage), then burning will tend to throw back the succession to an earlier stage, probably less useful, but careful grazing will maintain the better herbage. Should the Veld show indications of passing on to the rougher herbage of "Tambookie," then burning is required to check this and to maintain the *Anthistiria* stage. Grass-burning also increases the vernal plant societies, thereby adding to the colour effects; but this does not improve the grazing.

Grazing by stock also influences the herbage. An immediate effect follows on the selection of the finer grasses, which leaves the surface more exposed and favours extension of the more xerophytic species. A less obvious effect results from trampling of the soil, whereby the texture of the surface is deteriorated, and along tracks the run-off of water leads to formation of channels. The general result is to promote conditions favourable to pioneer and ruderal species, rather than the more stable types.

Within an abstract it is possible to indicate only a few main topics, in the present case plant succession has received attention. This may give the impression of vague references to a few outstanding genera, but the book itself must be used to fill up specific names, and to amplify the constituent species of the various plant societies. Again, the book is almost limited to grasslands, thus giving a somewhat one-sided outlook which requires compensation by reference to the author's earlier contributions on forest, bush and other plant communities.

W. G. SMITH.

NOTICES OF PUBLICATIONS OF GENERAL BEARING

THE PRACTICAL VALUE OF ECOLOGICAL RESEARCH

Hole, R. S. "Plant Oecology and its bearing on problems of economic importance in India," Presidential Address to the Section of Botany, Asiatic Society of Bengal. *Journ. and Proc. Asiat. Soc. Bengal*, **14**, 1918, pp. clvi-clxvii.

Cockayne, L. "The importance of plant ecology with regard to agriculture." *New Zealand Journ. of Science and Technology*, 1918, pp. 70-74.

Mr Hole's address brings out very clearly the great importance of ecological research to practical sylvicultural and other problems of land utilisation in India. Specific problems are cited, and the progress made towards their solution described. Thus we have the lack of adequate rejuvenation in the valuable Sal (*Shorea robusta*) forests of Dehra Dun and other parts of India. This has been shown to be due in some cases to lack of soil aeration (see notice of the author's work in present issue of the JOURNAL, under "Soil Aeration," p. 89), and in other cases primarily to drought. These two factors, however, interact, because on badly aerated soils the seedling roots are unable to penetrate during the rainy season below the top six inches of soil, and it is this top layer of soil which is dried out during the dry season, leading to the death of the seedlings. Lack of rejuvenation in teak (*Tectona*) forests is due to shading and the fire protection which prevents the opening of the forest to sun heat. The seeds appear to require a higher temperature for germination than they can get under these shade conditions. In 1911 it was shown that given types of soil naturally

bear parallel forest and grassland plant communities in India, just as in Britain¹, and this ecological fact is obviously an important guide to the choosing of land suitable for afforestation with given types of forest, and to the treatment required for the successful establishment of the forest when planted. Other problems of immediate practical importance to Indian forestry are the conditions under which various fungi attack the trees. In the case of root fungi like *Polyporus shoreae*, which attacks the Sal, and *Fomes lucidus*, which attacks *Dalbergia sissoo*, it is probable that defective aeration of the soil renders the roots of these trees peculiarly liable to the attacks of their respective parasites. It is particularly significant that the worst attacks of the *Fomes* occur in certain irrigated Punjab Sissoo plantations and of the *Polyporus* in the wet Sal forests of Bengal and Assam. The attacks of *Trametes Pini* on the Blue Pine (*P. excelsa*), which were at one time suspected of taking place through the roots, have been shown to be confined to wounds on the stem, and hence the fungus is prevalent only in those forests where lopping the pines for fuel or manure is a common practice. In the case of the "spike" disease of the Sandal (*Santalum album*) which is marked by local accumulations of carbohydrates in the leaves, and apparently allied diseases of other plants, it is suggested that the disease is a pathological condition determined by inadequate water supply or a similar factor, and experiments to settle the point are in progress.

It is clear that the problems involved in the cases cited concern the mycologist, the physiologist and the ecologist—often involving the work of all three. The importance of studying fungi in order to combat their attacks intelligently is now pretty generally recognised, and mycologists have been appointed by many governments and private corporations. But it is by no means generally recognised that the work of the physiologist and of the ecologist are equally essential if the problems presenting themselves are to be successfully coped with, so that practical action may be based on a thoroughgoing scientific knowledge of all the factors involved. In actual fact ecological problems generally lie at the root of the whole matter, as the author clearly shows, and in their own interests governments should appoint forest officers whose duty is to study in the first place the ecology of their forests, as well as mycologists and "practical" foresters. The "practical" sylviculturalist, it is true, often hits on an empirical "remedy" for the particular troubles he encounters, but in the absence of thorough scientific study he is very liable to attribute a result to a wrong cause (as for instance the lack of reproduction of a particular species of tree under shade conditions to the absence of light, when the true cause is defective aeration of the soil) and thus to be unable to apply his "remedies" discriminately.

The value of an ecological consideration of practical problems is not, of course, limited to forestry. As the author shows, a satisfactory study of the best method of exploiting grassland, whether for grazing or for paper-making, at once raises problems which require the ecological outlook for their proper solution. And the same applies to agriculture.

Dr Cockayne brings this out very clearly in the second paper cited above. He points out that "the yield of meat or butter-fat per acre is primarily a matter of the plant-covering of the farm," that "facts based upon the study of a virgin vegetation and on that of an artificial or modified vegetation are of equal value, the same laws governing both," and that "the ecology of virgin land is, then, the ecology of the farm, except that on the latter man can purposely alter the conditions to which the plants are subject in order to increase their economic efficiency." He concludes that "agriculture is neither more nor less than applied plant and animal ecology."

Now this conclusion is indubitable, but what those concerned with practical problems—farmers, local authorities and state governments—want to know, is not whether such a statement is theoretically true, but whether the actual investigations being made by

¹ *Indian Forest Memoirs. Bot. 1, 1911; Types of British Vegetation, 1911.*

working ecologists at the present time are likely to be of actual value to the farmer. Dr Cockayne points out that his own and Mr Foweraker's work on the succession of plant communities on shingly river beds forms the natural starting-point of work on the tussock grassland—true sheep country—produced as a result of the process, and that this might be made to show the wool-producing capacity of the tussock grasslands and how they could be improved. The author shows that there is still much ignorance concerning the actual relation to sheep of the mixture of races known collectively as *Poa colensoi*; and that even the life-histories of the two principal New Zealand tussock-grasses, *Festuca novae-zealandiae* and *Poa caespitosa*, are unknown, not to mention the effects of burning, under- and overstocking, and so on. Here is plenty of work for New Zealand ecologists, and we suggest that it would be a very good plan to turn some of them on to problems such as these which directly concern the farmer and thus demonstrate to the latter, in the most unmistakable way, the practical value of ecological research, by showing him how he can produce more wool. A few years of this sort of thing might produce an agitation among the farmers to have ecologists appointed to watch their farms.

In regard to dune culture Dr Cockayne shows that in the treatment of the New Zealand dunes empiricism is quite out of place, and that each type must be studied ecologically on its own account, till "rules for dune culture" can be drawn up for the benefit of agriculture.

Meanwhile there are signs of recognition on the part of state authorities. We learn that the Minister of Agriculture of the Union of South Africa has appointed an Advisory Committee for the Botanical Survey of the Union. The Committee includes such a well-known ecologist as Professor J. W. Bews of Pietermaritzburg, whose book on *The Grasses and Grasslands of South Africa*, an excellent example of the practical value of ecological work, is reviewed in the present number of this JOURNAL (p. 84), and the Survey will be under the direction of Dr Pole Evans, Chief of the Division of Plant Pathology and Botany of the Department of Agriculture. Professor Cowles's paper (see p. 120) read at the last meeting of the Ecological Society of America records the beginning of a systematic Forestry Survey of the State of Illinois along ecological lines, which is not only to record the extent and composition of existing forests but to advise on the reservation of natural history preserves and to determine areas which should be afforested or reforested.

Thus is ecology gradually beginning to come into its own.

STUDIES ON SOILS

SOIL AERATION

Howard, A. "Recent Investigations on Soil Aeration. Part I, with special reference to agriculture." *Indian Forester*, May, 1918, pp. 187–202.

Hole, R. S. *Ibid.* "Part II, with special reference to forestry," pp. 202–212.

The soil atmosphere is a subject which is clearly of great importance to plant ecology, first because it conditions the respiration of the roots of the higher plants, and secondly because it partly conditions the life activities of the soil micro-organisms, both aerobic and anaerobic, and these in their turn alter the chemical composition of the soil and thus influence the food of the higher plants. It is obvious that a loose coarse-textured soil will allow of freer gaseous diffusion between the soil interspaces and the atmospheric air than a firm fine-textured soil, and the behaviour of roots in sand and clay respectively show that the sand is better aerated to a greater depth. Hunter showed that, in the case of cress and wheat, root development varies directly with the looseness of texture of the soil in pot

experiments¹. But though botanists have long been familiar with these general relations comparatively little exact quantitative work has been done on the subject until quite recently.

The top six to twelve inches of soil on ordinary arable or pasture land has pore spaces forming ten per cent. of its total bulk, and the air in these spaces does not greatly differ in composition from atmospheric air. The oxygen content is somewhat less, say 18.5 to 20.5 per cent., and the CO₂ content generally markedly higher, varying from .01 to 3 per cent., as compared with 21 per cent. and .03 per cent. in the atmosphere. After heavy manuring with dung, or if the air is cut off by surface accumulations of water, the percentage of oxygen falls and that of CO₂ rises. Grassland soil atmosphere is also richer in CO₂ than that of arable land, and poorer in oxygen².

The interpretation of this condition is that the diffusion of air into ordinary well-cultivated soils is sufficiently rapid to maintain the gases of the soil atmosphere in nearly the same relative proportion as that in which they exist in the air, unless the plant roots and micro-organisms are taking up oxygen and giving off CO₂ at an exceptionally rapid rate. This is brought out very clearly in one of the curves given by Russell and Appleyard³, which shows that on dunged but uncropped land the percentage of CO₂ rises steadily to July, the period of greatest heat, the rise being presumably due to the activity of the micro-organisms, conditioned by temperature. On dunged land under wheat, on the other hand, there are two maxima, one in May when the plants are developing most rapidly, and the other in August at the time of the ripening of the grain. The former can be readily explained by the respiration of the rapidly growing roots, but the second rise has not been completely explained. Howard suggests that it may be partly due to the fact that the finer roots begin to die and decay after flowering is over, but this does not explain why wheat will not ripen properly if soil aeration is interfered with, a fact of experience in India. Thus in Northern India, where the soil is a fine alluvial silt, whose surface easily "crusts" as a result of irrigation and subsequent baking under the hot sun, it is found that while a second irrigation generally increases the crop yield, a third actually depresses it. At Quetta, where wheat is often irrigated six times on account of the dryness of the climate, the crop shows all the symptoms of poor soil aeration and dries up rather than ripens. The same factor is probably the cause of the slow ripening and bad filling of the barley grown on stiff soils in England. Similar effects are found in tobacco and cotton cultivation in India, the best results being only obtained where the soil aeration is above the average.

Hole shows that *Sal* (*Shorea robusta*) seedlings are readily killed when growing in a water-retaining soil, such as loam or leaf mould, in non-porous glazed pots, either by stopping up the drainage holes at the bottom or by covering the soil surface with a layer of dead leaves and thus decreasing evaporation. Germination and seedling development are also poor in the shade of the forest during the rainy season, and can be improved by felling strips of forest and letting in light and air. The effect is not however due to shading, since seedlings in pots of sand develop perfectly well in the same shade. The first symptoms are the blackening and death of the root tips, spreading eventually to the whole root system. The leaves at first remain healthy but eventually turn pale and droop. These symptoms occur when the soil is far from being saturated with water and there is still plenty of free air space near the roots. Water culture experiments show that the roots of *Sal* seedlings grow perfectly well when air is allowed access to the culture solution. But water held in contact with forest loam becomes heavily charged with CO₂ (for instance, they show in

¹ Hunter, C. "Some observations on the effect of soil aeration on plant growth." *Proc. Phil. Soc. Univ. Durham*, 4, 1912, pp. 183-186.

² See Russell, E. J. *Soil Conditions and Plant Growth*, 1917, p. 142.

³ *Journ. of Agric. Science*, 8, 1917, p. 385 (noticed in this JOURNAL, 6, p. 231).

nineteen days a rise from 5 to 163 mg. per litre) and also decreases in oxygen content (4.8 to 1.2 mg. per litre in the same period) apparently owing to the activity of soil organisms. By bubbling CO₂ through culture solutions in which Sal seedlings are growing Hole found that a concentration of 500 mg. per litre blackened and killed the root tips, whose appearance resembled that of seedling roots grown in badly aerated soil. This is a concentration very much above that found in percolation water from soil in which the seedling roots were killed, but it is believed that the local concentration of the gas in soil water may reach much higher figures. Further, the deficiency of oxygen which accompanies the increase of CO₂ almost certainly co-operates in the result. (Cf. Kidd's experiments in which 9 to 12 per cent. CO₂ inhibited the germination of seeds with 5 per cent. of oxygen present, while 20 to 25 per cent. were required with 20 per cent. of oxygen. *Ann. of Bot.* **31**, 1917, p. 457.)

It is shown by Hole that the texture of the soil is an important factor. Thus the root development of Sal seedlings is very much better in coarse than in fine loams, and Sal does not flourish in really wet forests except where the soil is sandy or gravelly. Marriott has ascribed the poor growth of older trees to deficiency of soil aeration and suggests that during the wet season the trees may practically cease to grow, whereas with proper aeration, growth ought to be most active during the rains.

Hole makes the interesting suggestion that the well-known toxic effect of grass roots on fruit trees established by Pickering may be due to the carrying down of the abundant CO₂ produced by the densely matted fine grass roots to the roots of the trees, and calls attention to Pickering's statement that the toxic effect of the percolation water disappears when the water is exposed to the air for twenty-four hours. He also suggests that the evil effect on plants of soils rich in organic matter in which protozoa have accumulated in large numbers may be brought about by the effect of the CO₂ produced by the protozoa on the roots of the plants.

The results of the researches briefly described above may be recommended to the attention of ecologists who are studying the soil factors of various plant associations. Cannon and Free (see this JOURNAL, **5**, p. 127) consider that the zonation of vegetation round the dry lake basins of the arid regions in the United States and its absence in the bottoms of the basins are possibly correlated with the different aeration requirements of the different species, and the same factor may well be important in our wet moorland, salt marsh, and similar habitats. Jefferies¹ showed that on moorland near Huddersfield *Molinia coerulea* colonised positions—streamsides and "flushes"—in which its roots would presumably obtain more oxygen than they would on stagnant moorland occupied by *Eriophorum vaginatum*, but he did not attempt to separate this factor from the acidity of the soil. We want more experiments in growing "key" plants like *Nardus*, *Molinia* and *Eriophorum* under controlled conditions in relation to these factors, as well as practicable field tests for roughly estimating the oxygen and CO₂ contents of soil waters.

PALAEOZOIC SOILS

Robinson, Gilbert Wooding. "Studies on the Palaeozoic Soils of North Wales." *Journ. Ag. Science*, **8**, Part 3, pp. 338-384, 1916-17.

A detailed field and laboratory study of a number of typical soils derived from the weathering of palaeozoic rocks in the counties of Anglesey, Carnarvon and Denbigh, including also those derived from the weathering of local glacial drift and the associated sandy, alluvial and peaty soils. The soils were found to differ, not only genetically, but also in their properties and constitution, from soils hitherto studied in this country.

¹ This JOURNAL, **3**, 1915, p. 93.

Apart from blown sand, alluvium and peat, the soils are grouped as Anglesey Medium Loam (derived from Precambrian metamorphic gneisses and schists), Palaeozoic Silt Loam (derived from Silurian and Ordovician shales and flagstones), and Carnarvonshire Stony Loams (a variable series of gravelly or stony medium loams formed of material scraped down from the mountains by local glacial action). All these soils are of a loam texture, the clay fraction rarely exceeding 7 to 10 per cent., though with the high rainfall the heavier ones present to the cultivator the difficulties of clays. When reasonably dry they are easy to work. The silt fraction is high, but even the fine silt does not contribute to the plasticity of the soil, as was shown by removing the clay fraction from a silt-clay glacial soil, when the plasticity was reduced to nil. If plasticity be attributed to the presence in soils of hydrated colloids, the general absence of plasticity in these Palaeozoic soils could be explained by the general metamorphism ("regional" in the case of the old Palaeozoic sediments) resulting in the destruction of the colloids present in the original muds and clays. Another characteristic of these soils is the remarkably high proportion of fine gravel, usually by far the smallest fraction except in the case of sands.

An important feature is that the coarser fractions mainly consist of undecomposed parent rock and therefore show a higher percentage of alumina and ferric oxide and a lower percentage of silica than do the coarser fractions of English soils: the fine fractions also show a higher percentage of alumina and ferric oxide than do those of English soils. It is suggested that the more siliceous the parent rock the larger are the particles with the highest silica content. These soils form a class similar to Ramann's Steinböden, consisting of but slightly decomposed rock fragments. Potash is fairly high, phosphoric oxide not low, organic matter high, and lime very low.

Ecologists have long recognised that the obvious differences between the soils of the mountainous palaeozoic regions of the west of Great Britain and those of the hills and lowlands of the rest of the country might be partly responsible for the differences in native vegetation. The coincidence of a corresponding difference of climate however renders the separation of the edaphic and climatic factors difficult. Mr Robinson's work affords welcome data from which a start might be made towards a solution of this problem.

CHEMICAL WORK ON SOILS (M.C.R.)

Russell, E. J. and Appleyard, A. "The influence of Soil Conditions on the Decomposition of Organic Matter in the Soil." *Journ. Ag. Science*, **8**, Part 3, p. 385.

The biochemical decomposition of plant residues and other organic matter in the soil is of fundamental importance for soil fertility. These changes have been studied extensively in the laboratory, but there has as yet been little work in the field on the relation between bacterial activity and the extent of the change. Dr Russell and Mr Appleyard have made a prolonged study extending over three seasons of the changes taking place in a single plot and have estimated how far, and in what way, the rates of decomposition can be related to the changes in bacterial numbers. The method adopted was to determine the changes in bacterial numbers, in nitrate content of the soil, and in CO₂ content of the soil air on five different plots at frequent and regular intervals.

They find that there is sufficient resemblance between the curves for bacterial numbers, CO₂ content (except for a period on cropped land) and amount of nitrate to justify the conclusion that they are all related.

The biochemical decompositions in the soil are determined, as might be expected, in the first instance by the temperature, and do not proceed to any notable extent below 5° C. As soon as the temperature rises action begins rapidly, but soon slows down as other

factors begin to operate. Moisture and rainfall are shown to be important factors, especially the latter, and it seems probable that the dissolved oxygen carried down in rain has an important effect on bacterial activity. The growing crop exerts a depressing effect, though whether by using up oxygen, by giving out CO_2 or by some other action is not clear.

The paper is accompanied by a number of excellent graphs.

Stewart, Guy R. "Effect of Season and Crop Growth in Modifying the Soil Extract." *Journ. Agric. Research*, **12**, No. 6, p. 311.

The author of this paper gives a comprehensive historical review of earlier work on the water-soluble material of soils. He draws attention to the contradictory nature of the results of such work and defines as the subject of his own investigation: (1) the relationship between the soluble soil nutrients in cropped and uncropped soils; (2) the relationship between the soil extract and the crop produced thereon.

All the experimental work was done on fresh soils, a uniform procedure of extraction being adopted, and the author considers that the fluctuations observed in the water extract reflect actual changes in the soil solution. Of the conclusions drawn the following may be specially noted:

1. Notable differences were observed between the amounts of nitrates, calcium, potassium and magnesium present in the water extracts from cropped and uncropped soils.
2. The phosphates did not exhibit corresponding differences. Great dissimilarities in phosphate content were observed in different soils, but in any one soil the amount was practically constant in both cropped and uncropped plots.
3. Striking differences occurred between the soluble nutrients present in the various uncropped soils.
4. The three poorest soils yielded the smallest amounts of water-soluble nutrients and the smallest differences between the cropped and uncropped duplicates. This last result is notably at variance with the earlier statements of Whitney and Cameron (1903).
5. By comparison with freezing-point determinations the concentration of the soil solution calculated from the water-extract was shown to be from two to four or five times as great as that of the actual soil solution. From the results of freezing-point determinations it is concluded that variations in the water-extract reflect actual changes in the soil solution.

The inclusion of a large number of graphs showing seasonal variations in the amounts of calcium, potassium, magnesium, nitrogen and phosphate in water extracts of the soils studied and an unusually comprehensive bibliography give this paper an additional value for purposes of reference.

Hutchinson, R. H. "Soil Acidity as Influenced by Green Manures." *Journ. Agric. Research*, **13**, No. 3, p. 171.

Experiments reported in recent years have shown that soils of experimental plots treated continuously with artificial fertilizers in which the nitrogen is supplied as ammonium sulphate become acid in reaction, and that the crop-yields of such soils fall off in proportion to the degree of acidity. It has also been shown that such soils can be brought back into normal bearing by the addition of lime or limestone in sufficient quantity to neutralize the acidity. Using soil from an experimental plot already acid from the addition of artificials containing ammonium sulphate, experiments were carried out to determine changes in acidity due to the addition of fresh green manures. The results of such experiments showed in general that fresh green manures ploughed into such a soil, at first reduce its acidity but finally leave it in a more acid condition.

They demonstrated also that, given suitable conditions of moisture, temperature, etc., nitrification goes on vigorously in such soils and that green-manured soils are rich in nitrates despite the soil acidity.

Millar, C. E. "Relation between Biological Activities in the Presence of Various Salts and the Concentration of the Soil Solution in Different Classes of Soil." *Journ. Agric. Research*, **13**, No. 4, p. 213.

It has been shown that certain salts, present naturally in soils or added as fertilizers, have marked effects on their bacterial flora. The causes of such effects are at present incompletely known although it has been assumed that toxicity and osmotic pressure changes are probably directly concerned in them.

The paper under consideration gives an account of experimental work bearing on these problems carried out at the Michigan Agricultural College Experimental Station. Three soils of widely different type were selected and the degree of biological activity estimated by determining the rate of ammonification of dried blood. Experiments showed that the effect of different salts was greatly modified by the nature of the soils to which they were added, and also that the addition of dried blood has an appreciable effect on the osmotic pressure of the soil solution. On the basis of these experiments it seems improbable that osmotic pressure is the governing factor in variation of biological activity in soils, in so far as this is related to constitution and concentration of the soil solution.

Plummer, J. R. "Studies in Soil Reaction as Indicated by the Hydrogen Electrodes." *Journ. Agric. Research*, **12**, No. 1, p. 19.

During the last few years a voluminous literature has accumulated dealing with the subject of soil reaction.

The significance of the terms "true acidity," "true alkalinity," and "true neutrality" as used by the author is defined as follows:

"Pure water dissociates into H and OH ions in equal concentration. The product of the concentration of these ions is a constant approximately 1×10^{-14} . When the H ions are present in a concentration greater than 1×10^{-7} the solution is acid; the presence of OH ions in greater concentrations than 1×10^{-7} results in an alkaline solution." Using a number of untreated soils in suspension it was found that the H ion concentration varied from almost "true neutrality" to rather excessive "true acidity." With the Morgan apparatus for extracting film water from soils it was shown that the reaction of the film water was the same as that of the free water, differing only in intensity.

The effects of certain fertilizers on the H ion concentration of plots long-treated were as follows:

1. Ammonium sulphate materially increases the H ion concentration and the acidity resulting therefrom often extends to the subsoil. Acidity due to the use of sulphate of ammonia was more intense in the film water than in the free water of three soils.
2. Nitrate of soda slightly reduced the acidity of the plots to which it was applied.
3. Potassium sulphate increased the "true acidity," but in less degree than sulphate of ammonia.
4. Acid phosphate did not appear to affect the H ion concentration of field soils.
5. Lime materially increased the OH ion concentration of field soil to which it was added.

Hoagland, D. R. and Sharp, L. T. "Relation of Carbon Dioxide to Soil Reaction as Measured by the Hydrogen Electrode." *Journ. Agric. Research*, **12**, No. 3, p. 139.

The authors refer to their previous paper on soil reaction as determined by the hydrogen electrode (see Notice, this JOURNAL, **6**, p. 232). In considering the effect of carbon dioxide on soil reaction an earlier investigator (MacIntire, 1916) states that many acid soils when extracted with water saturated with carbon dioxide yield *alkaline* extracts and draws the following conclusion: "Since we admit that the soil solution is the medium through which a plant absorbs its mineral supply, we are compelled to conclude that a plant's source of nutrition is almost always alkaline, but of varying degrees of alkalinity."

The experiments recorded in the present paper were undertaken in order to obtain direct evidence on the influence of carbon dioxide on soil reaction, and may be briefly summarized thus:

The H ion concentration of suspensions of acid soils is not markedly affected by increasing the content of carbon dioxide up to 10 per cent. The H ion concentration of slightly alkaline soils is slightly increased by such treatments. A notable increase in H ion concentration is observed when soils containing alkaline carbonates are similarly treated.

It has not been found that any treatment with carbon dioxide can produce an alkaline reaction in the suspension of an acid soil. When the original conditions are restored, no permanent change in reaction could be attributed to the carbon dioxide. The authors hold that their experimental data can be effectively applied to field soils, assuming that the values found by Russell and Appleyard (1915) for carbon dioxide content of the soil atmosphere may be regarded as typical. Their conclusions are entirely at variance with those of MacIntire quoted above as to the effect of carbon dioxide concentration on soil reactions.

Hoagland, D. R. "The Freezing Point Method as an Index of Variations in the Soil Solution due to Season and Crop Growth." *Journ. Agric. Research*, **12**, No. 6, p. 369.

This is a study of the same soils as those used by Stewart (p. 93) in his investigations on the effect of season and crop growth on the soil extract, having in view the importance of correlating the data deduced from the use of soil extracts with those based on the actual soil solution in each case. The procedure consisted in determining the depression of the freezing point in the soil itself under varying moisture conditions, attempts to obtain an appreciable quantity of solution from soil containing the optimum amount of moisture having already proved fruitless.

Such experiments have considerable interest for the plant physiologist since they allow comparison between the osmotic pressures in nutrient solutions and those in the soil solution as it actually exists in the soil under conditions favourable to crop growth. The experimental results show that the osmotic pressures existing in the soil are those most favourable to the growth of barley in culture solution.

It was found that in general the growth of a crop causes a marked diminution in the concentration of the soil solution, and also that soil solutions under conditions favourable to plant growth are very dilute, especially at the height of the growing season.

Certain general agreements between the extraction and the freezing-point methods are discussed. It may be pointed out that the results of Hoagland, like those of Stewart (*loc. cit.*), are in complete disagreement with the earlier views expressed by Whitney and Cameron on problems relating to the soil solution.

Miller, C. F. "Inorganic Composition of a Peat and of the Plant from which it was formed." *Journ. Agric. Research*, **13**, No. 12, p. 605.

Comparison of the inorganic composition of a peat and of the material from which it was formed was undertaken in a case in which accumulation of the remains of one plant species only, viz.: *Cladium effusum* (saw grass), was responsible for peat formation. Assuming that no silica was lost during the change, about seven parts of *Cladium* were required to yield one of peat.

Based on this assumption it is calculated that the plant constituents were leached to the following extent: iron oxide and alumina 12.2 per cent., lime 24 per cent., magnesia 41 per cent., potash 96 per cent., soda 84 per cent., phosphoric acid 70 per cent., nitrogen 33 per cent.

Hills, T. L. "Influence of Nitrates on Nitrogen-assimilating Bacteria." *Journ. Agric. Research*, **12**, No. 4, p. 183.

The importance of nitrogen for plant life can hardly be over-estimated, and this fact is well brought out by the almost innumerable investigations which have been made concerning the source of nitrogen for plants. The influence of nitrate nitrogen on various plants has been the controlling idea in many of these experiments and but little attention has been given to the effect of nitrates on the lower organisms, especially bacteria.

It seems clear, however, that progress in the knowledge of soil-fertility depends on a study of the effect of nitrogenous fertilizers on the soil micro-organisms as well as on the higher plants. The action of fertilizers on the different groups of soil organisms, the relation of these organisms to the higher plants, and recognition of the more important groups are some of the factors involved in the problem of soil fertility. The author of the paper cited records the results of an investigation into the effect of nitrates on soil bacteria, especially those concerned with the fixation of atmospheric nitrogen. Two distinct lines of investigation were pursued:

(a) The influence of nitrates on *Azotobacter*, with reference to growth of the organism in soil and its nitrogen-fixing powers.

(b) The action of *B. radiculicola* on nitrates in solution, and the possible nitrogen-assimilating powers of the legume in the presence of nitrates.

The following results may be noted:

Azotobacter. The addition of small quantities of K, Na, and Ca nitrates caused a great increase in the number of bacteria in sterilized soil. K and Na nitrates caused an increase, Ca nitrate a decrease in the amount of nitrogen fixed by *Azotobacter* on agar films. Under aerobic conditions *Azotobacter* assimilated atmospheric nitrogen more rapidly in the presence of nitrate than in its absence.

B. radiculicola. Small quantities of K, Na, Ca, and NH_4 nitrates increased the number of bacteria in soil. Under aerobic conditions the amount of atmospheric nitrogen fixed was not materially affected by the addition of nitrates.

Extremely interesting results were obtained from a study of the influence of nitrates on the formation and re-formation of nodules on alfalfa roots. It was found that: (a) the presence of nitrates is detrimental to the formation of nodules by alfalfa; (b) the non-formation of nodules is not due to a weakening of *B. radiculicola*, which grows vigorously in the presence of nitrates; (c) some reaction takes place between the plant root and the nitrates inhibiting formation of nodules; (d) nitrates in the soil prevent the re-formation of nodules once removed and cause a decrease in the number of those already present.

Gainey, P. L. "Effect of Paraffin on the accumulation of Ammonia and Nitrates in the Soil." *Journ. Agric. Research*, **10**, No. 7, p. 319.

Paraffin wax has been widely used in the study of soil biology, soil fertility, plant physiology and kindred subjects, e.g. in the *paraffin wire-basket method* of studying soil fertility; for supporting seedlings in culture solutions, etc. Paraffin oil has also been used in the separation of soil solutions (Giltner, 1913). The authors made use of the commercial preparation, *Parawax*, and subsequently of pure paraffin-wax in certain soil experiments and noticed a marked inhibitory effect on the accumulation of nitrates in the soil. These observations led to further investigations which showed conclusively that paraffin cannot be safely used in any investigations unless the microbial flora is absolutely under control as regards the species present.

In experiments carried out by the authors the presence of paraffin, whether as wax, *Parawax*, or oil, completely inhibited the accumulation of both ammonia and nitrates in soil, whether the paraffin was mixed with the soil or only surrounded it. In soil to which cottonseed meal was added as a source of nitrogen, ammonia and nitrates were rapidly formed in the presence of paraffin and as rapidly disappeared. Parallel with the disappearance of active nitrogen there was a disappearance of paraffin and an enormous development of certain species of fungi. The disturbing effect is due not to an inhibitory effect of paraffin on ammonifying and nitrifying organisms, but to the rapid consumption of ammonia and nitrates by organisms stimulated by the presence of paraffin and for which it provides a source of carbon and energy.

If nitrogen compounds were not added to the soil, available nitrogen soon becomes the limiting factor in fungus growth. If ammonia sulphate or cottonseed meal were added, the cultures at the end of four weeks' growth appeared to be almost solid masses of white hyphae.

It is maintained by the authors that their results offer a satisfactory explanation of the failure of the *wire-basket method* in the hands of some investigators, and discount the value of all results hitherto reported where paraffin has been used in physiological or cultural experiments involving mixed cultures possibly containing organisms capable of utilizing paraffin in their metabolism.

SOIL WATER (M.C.R.)

Harris, F. S. "Movement and Distribution of Moisture in the Soil." *Journ. Agric. Research*, **10**, No. 3, p. 113.

Ever since agriculture has been the subject of scientific study, soil moisture in its various relations has been given a great deal of attention. In this paper which presents the results of thousands of determinations an attempt has been made to throw light on a number of the important phases of soil-moisture movements. Most of the results are presented in diagrams which make relations more apparent than does the study of long tables in which the figures are so difficult to analyse that the reader seldom sees more than the most apparent relationships. The paper includes a short account of the historical development of soil-moisture studies and a full bibliography of previous papers on the subject. The author summarizes his own experimental results under twenty-three heads but it is not possible to deal satisfactorily with these results in a brief notice. They were deduced from *field* studies on the effect of fallow, kind of crop, manure, irrigation water, surface mulches, cultural methods and seasonal conditions on the movement and distribution of soil moisture, supplemented by *laboratory* experiments to determine the effect of initial percentage of moisture, gravity, soil type, source of supply and other variables.

Alway, F. A. and McDole, G. R. "Relation of Movement of Water in a Soil to its Hygroscopicity and Initial Moistness." *Journ. Agric. Research*, **10**, No. 8, p. 391.

The rate and distance of capillary rise of water in soils have been determined in many laboratory investigations, although, where the ground water is at a considerable distance below the surface, as is generally the case, these factors appear to be of little practical importance. On the other hand, the downward penetration of definite amounts of water has received very little attention. In experiments on both these subjects the soils have usually been employed in the air-dry state, a condition rarely met with in nature and in none of the experiments has the relative hygroscopicity of the soils been taken into account. In the paper under consideration the authors have considered the hygroscopicity—as expressed by their hygroscopic coefficients—the initial moistness of the soils, and have also determined the moisture-equivalents. Among other results obtained from experiments with seventeen soils, ranging from a coarse sand to a silt loam, it was found that the rate of penetration showed little dependance upon the hygroscopicity, but was definitely affected by the moistness; the higher the initial moisture content of any soil within the limits employed, the more rapid being the downward movement of water. With the finer textured soils the water content of the moistened layer was not distinctly affected by the initial moistness, but with the coarser members the drier the soil the wetter was the moistened layer. Provided that a period of high evaporation is to precede the next rain, the character of the weather immediately following a rain will have a greater effect upon the loss of moisture by evaporation in the case of a coarse than of a fine-textured soil. It was also shown experimentally that the relative rates and distances of percolation in the different soils do not correspond to the relative rates and heights of capillary rise.

CONCEPTS AND NOMENCLATURE OF VEGETATION

Gams, Helmut. "Prinzipienfragen des Vegetationsforschung. Ein Beitrag zur Begriffsklärung und Methodik der Biocoenologie." *Vierteljahrsschr. d. Naturf. Ges. in Zürich*, 1918, pp. 293–493.

Dr Gams has come to the conclusion that synecological or, as he calls it, biocoenological nomenclature is in a hopeless muddle, and he aspires to clear up the mess by abolishing nearly all the old terms and propounding a new set. Many people have arrived at the same conclusion and not a few have had the same aspiration. But it is seldom that an advance can be made by wholesale "scrapping" and reconstruction. Organic growth, in this as in other spheres, is brought about by gradual change and adaptation. The fitness of terms is tested by continual use and in no other way. Thus the author wishes, as others have wished before him, to abolish "formation" and "association" on the ground that they have been and are still to some extent used in different senses by different writers. But the terms still continue to be used. They have come, it may safely be said, to stay, because in spite of some differences of use they actually serve a useful purpose and correspond with necessary concepts. These concepts are gradually attaining greater clearness of form and will presently be susceptible of something like precise definition. In the case of an exceedingly difficult and elusive subject like synecology (or biocoenology) this is the only possible history of terms and concepts. One could wish that writers on the subject would cultivate a more vivid sense of reality in these matters.

Meanwhile Dr Gams is a clear logical thinker, and contributes some incisive criticism and lucid discussion, which are well worth perusal, of various ecological conceptions and

descriptive terms. His main constructive suggestion in regard to concepts is that two types of units should be distinguished, the ecological and the topographic, which are often confused and mixed. The former he calls *synusia* (the Greek equivalent of "associations") and distinguishes three grades: (1) where the independent components are of the same species, (2) where the independent components are of different species belonging to the same class of life form and showing the same series of "aspects," (3) where the independent components are of different classes of life form and show different series of aspects, but are united into an ecological unit in a single habitat by fixed correlation. Thus in a pinewood the trees of *Pinus sylvestris* would form a synusium of the first grade, together with *Viscum* and *Cnethocampa* (the Processional caterpillar) living on the pines because they are not independent, but not including *Stereodon* on the trunks of the pines because the lichen grows equally well on rocks or on the earth. The *Calluna* and *Vaccinium* growing on the floor of the wood with *Hypnum Schreberi* and *Cladonia* would form a synusium of the second grade because they are different species but all independent chamaephytes. With *Deschampsia flexuosa* and *Melampyrum pratense* a synusium of the third grade would be formed, because these plants belong to different classes of life form. This third grade of synusium corresponds roughly with the "association" of most authors. If all the habitat conditions of two areas within distinct floral districts are the same the life forms and aspects will be the same but the lists of species will be different. Synusia showing these resemblances and differences the author groups together as *isocies*, for instance Mediterranean maquis and Californian chaparral, or the beech forest of the eastern United States and of western Europe. For the topographical unit Dr Gams adopts the word "biocoenose" (introduced by Möbius in 1877 and since used by various animal ecologists) which we may transcribe *biocoenosium* or *phytocoenosium* for the vegetation of any unitary habitat, which will include several and often many plant and animal synusia (ecological units) of the first to the third grade. Biocoenosis of different regions which are compounded of isocies are called *isocoenosis*. The author discusses the question whether a wood of definite type is to be considered a synusium of the third grade or a phytocoenosium, and decides in favour of the latter alternative, i.e. that a wood is a topographical not an ecological unit, on the ground that no species of the ground flora is confined strictly to one kind of wood, and that a ground species may not only occur in any wood in which the shade is approximately of the same degree but may also be found in caves and under overhanging rocks where the light is of the same intensity as in a wood. Similarly most meadows, and also fens and moors, are to be considered, according to the author, topographical rather than ecological units.

The author rejects the attempt to classify vegetation units on "dynamic" lines. He is particularly scornful of Clements's conception of the formation as an organism with a definite development, and hardly less so of that author's detailed scheme of classification. It may be admitted that the comparison with the development of an organism may be carried too far: there are certain features in which there is a correspondence and there are others in which there is no correspondence; but in regard to Clements's concepts and nomenclature as developed in *Plant Succession* it is noteworthy that two recent workers (Pearson, in this JOURNAL, 1917, 1918, and Bews, *The Grasses and Grasslands of South Africa*, 1918, see review in the present number of this JOURNAL, p. 84) have been favourably impressed by Clements's scheme, and have successfully applied it respectively to two very different types of vegetation.

Dr Gams's sharp distinction between synecological classification (synusia) and topographical classification (biocoenosis) certainly has a logical justification. He successfully shows that the units mostly dealt with by ecologists are topographical, but he does not contribute much towards the practical task of characterising, delimiting and classifying

these biocoenosis: indeed he scarcely takes cognisance of the ecological factors which unite and separate the smaller topographical units. The practical difficulty comes in when we attempt to separate the author's third grade of synusia, the components of which "durch feste Korrelationen zu einer ökologischen Einheit auf einem einheitlichen Standort verbunden sind," from what the author regards as purely topographical units. The whole difference depends, as will be seen, on the degree of correlation. The word "feste" rather begs the question. Whether the distinction, logically sound though it is, will be useful in practice, remains to be seen.

The author gives a new classification of life forms, largely based on Raunkiaer's system, but extended and including animals. This appears to be the best which has yet been published.

Du Rietz, C. E. "Några synpunkter på den synekologiska vegetationsbeskrifningens terminologi och metodik." *Svensk Botanisk Tidskrift*, **11**, 1917, pp. 51-71, with a German résumé.

In this paper the author puts forward several new terms and provides definitions for several old ones. His general standpoint is that of the paper noticed below, and his terminology may be considered as superseded by that proposed by the joint authors.

Du Rietz, C. E., Fries, Th. C. E., and Tengwall, T. Å. "Vorschlag zur Nomenklatur der soziologischen Pflanzengeographie." *Svensk Botanisk Tidskrift*, **12**, 1918, pp. 145-170.

This paper sets out to expound, modify and summarise the ideas originating with Hult (1881) and Sernander, who worked on Finnish vegetation, and recently developed by Fries and Du Rietz in Sweden. The authors lay stress on the separateness of the Finnish-Swedish school of ecologists from the workers in the rest of the world, and claim that the former was marked by true 'inductive' methods at a time when extra-Swedish study of vegetation was suffering from a conflict between confused 'inductive' principles and the 'deductive' principles introduced by Schouw, Thurmann and Sendtner. They insist that the plant-association must be characterised by the composition of the vegetation alone, i.e. by definite floristic composition, and that the factors which give rise to associations must not be introduced into the definition, and combat the views of Samuelsson and Melin, who include in the same association similar "Bestände" which may have no species in common. The authors proceed to call attention to the historical factor, which, together with the 'ecological' (habitat conditions) and the biotic, helps to determine the associations actually existing in a given area. Thus successful invasion by a foreign species may occur without any alteration of the habitat, and several associations may exist side by side in the same habitat.

All this of course is perfectly true, but the authors seem to ignore the range of conditions within which an association can exist, which is an essential datum for determining what may be called the ecological constants of the association. The whole paper seems vitiated by the belief that 'inductive' is synonymous with 'descriptive.' The authors rightly contend for an accurate floristic characterisation and limitation of the association, but one of the main objects of synecology is surely to define the conditions under which given associations develop, exist and die out. If that can be accurately done it forms part of the characterisation of the association, and to stigmatise all attempts to take the habitat into consideration in classifying vegetation as the employment of 'deductive' methods appears to be a simple misuse of language. We fully agree however that the association must *in the first instance* be defined by its floristic composition, and not by habitat, and

that to *name* an association as the association of such and such a habitat is to begin at the wrong end. Some of the newer definitions of synecological terms given by the authors may be summarised as follows:

Association-fragment. A plant-community which cannot form an elementary association on account of restriction of the habitat.

Facies. Various forms of an association due to geographical position.

Variants. Deviations of associations due to other than geographical causes.

Association-complex. A union of associations or fragments of associations to a phytogeographical unit. (Cf. Nichols's use of the same term, p. 102 below).

Twin-associations (*Zwillingsassoziationen*). Associations floristically and physiognomically corresponding in one or certain layers only. (The conception of a 'Zwillingsformation' was introduced by Hult.)

The authors accept Warming's concept of the formation and adopt Drude's conception of 'elementary associations' (see this JOURNAL, 2, p. 52).

The authors are concerned also that more respect should be paid to priority in the use of the terminology of vegetation. In this matter we fear they will not meet with a great deal of sympathy. If there was one point on which all the phytogeographers present at the Brussels Congress of 1910 were agreed it was that there must be no fixation of terminology until general agreement was reached. It is perfectly clear that the failure to reach general agreement means that the development of concepts is still incomplete, that various points involved in the concepts employed are still obscure, and it is quite futile to attempt to fix nomenclature while that is the case.

Nichols, George E. "The interpretation and application of certain terms and concepts in the ecological classification of plant communities." *The Plant World*, 20, 1917, pp. 305-319 and 341-353.

In sharp contrast with the authors whose papers have been noticed above Nichols takes the principle of succession as the groundwork of his classification. He regards the association as the fundamental unit of vegetation, but unlike the Swedish authors defines it as the group or community of plants occupying a common habitat, which again he defines as a unit area with an essentially uniform environment. These definitions at once introduce the difficulty of what is to be considered an 'essentially uniform' environment, as to which difference of opinion is often acute owing to the great complexity of the interactions of the factors involved. We agree with the 'floristic school' in preferring to define the association by its floristic and vegetational composition. Broadly speaking we all know an association when we see one, or rather when we have had some little experience of it and its neighbours, just as broadly speaking we all know a species in the same way. In both cases there may be differences of opinion as to just how much either should include, as to whether we should count a well-marked facies correlated with a difference of habitat as a distinct association, or whether we should separate a well-marked variety as a distinct species. We are impressing our concepts on nature in both cases, but they are good workable concepts for all that, because there is, ordinarily, a certain discontinuity between the types of well-marked associations as between the types of well-marked species. But the habitat cannot yet be defined so closely in terms of its ultimate elements, and we therefore do well to start with the unit of vegetation itself as defined by floristic composition and by structure. The author accepts Clements's consociations (alternative dominants) and societies (local aggregations of species of secondary importance), as units subordinate to the association, but considers these as floristic rather than ecological units since they are not as a rule correlated with marked differences of habitat. He also distinguishes *habitat-types*

formed from parallel series of habitats, and corresponding *association-types* formed from the series of associations which inhabit them.

In considering the successional relations of associations Nichols postulates a regional climax association-type, which has attained the highest degree of mesophytism which the climate of the region permits, but he dissents from the assumption commonly made or implied by American ecological writers that all the vegetation of a climatic region is on its way to approximate to that type. He says it is untenable in the light of many years of field experience and fails either to accord with theoretical considerations or to harmonise with observed facts. He contends that while the climatic climax is reached on the most favourable soils the edaphic influences of less favourable soils are limiting factors in succession, that they not only determine its rate but its extent. He thus arrives at the conception of an *edaphic climax association* which is prevented from reaching the climatic climax by the edaphic factors of the habitat. As a good case of such an edaphic climax the New Jersey pine barrens are cited. This well-known area has been uninterruptedly out of water since Upper Miocene times, but while it is situated in a climatic region of deciduous forest, it has never got beyond the pine stage of succession on account of the nature of the soil.

The author also puts forward the related concepts of the *habitat-complex* and the *association-complex*, formed by the different related habitats and corresponding associations existing within a physiographic unit area, as for instance, a pond, a burned area and so on. Such a habitat-complex is a physiographic entity of a higher order than the single habitat, and the association-complex is similarly an ecological entity of a higher order than the single association. This ecological unit the author identifies with the *edaphic formation*, covering the whole series of successional stages actually met with in the physiographic unit area. Thus Nichols's "edaphic formation" corresponds with Moss's "formation," and his "edaphic climax association" with Moss's "chief association."

Mr Nichols also recognises *edaphic formation-types* and *edaphic formation-complexes*, concepts built up in a similar way to those of the corresponding combinations of associations. The edaphic formation-complex of a climatic region corresponds, in this terminology, with the *climatic formation*. Finally we have the *climatic formation-type*, which includes all climatic formations determined by similar climates, such as the often cited case of the sclerophyllous Mediterranean and Californian vegetation, the deciduous forest of the eastern United States and of Western Europe, the short grass of the American Great Plains and of the Russian steppes, and so on. The author concludes his paper by an application of his system to the vegetation of the northern Cape Breton region, which he has particularly studied.

NOTICES OF PUBLICATIONS ON BRITISH VEGETATION

Paulson, R. "Notes on the Ecology of Lichens, with special reference to Epping Forest." *Essex Naturalist*, **18**, 1918, pp. 276—286. 3 plates.

The author shows that the lichen flora on the bark of hornbeams (*Carpinus betulus*) in Epping Forest differs from that on oakbark and includes sixteen species, of which eight are shade lichens belonging to the Graphidiaceae, a family very poorly represented in the oakwoods of the same neighbourhood. Where this family occurs on oaks it is on the bark of young trees (usually *Q. sessiliflora*) fifteen to twenty-five years old, before it has become deeply furrowed. The growth of the lichens prevents the furrowing of the bark over the

portions they occupy. The Graphidiaceae on oakbark gradually give place to Parmeliaceae (*P. physodes*, *P. sulcata* and *P. borrieri*). The trunks of *Q. robur* on the London Clay are singularly bare of any epiphyte except *Protococcus viridis* Ag. (*Pleurococcus vulgaris*), and this is said to be a general phenomenon. Hence the author concludes that the lichen flora of *Carpinus* adds another feature to those which separate hornbeam wood from oakwood. He recognises two factors at work—the smoothness of the bark of the hornbeam and the relatively deep shade. The terricolous lichens of hornbeam wood are similar to those of oakwood though not so numerous or luxuriant.

The beechwoods (*Fagus sylvatica*) of Epping Forest have not an abundant lichen flora, though it is better developed than that of the chalk beechwoods of Hertfordshire and Buckinghamshire. *Lecidea crustulata* and *Rhizocarpon confervoides* on the pebbles among the beeches represent the group of saxicolous lichens occurring on the flints of the chalk beechwoods.

Betula has few lichens on its bark, probably because of the rapid exfoliation, except towards the base where the bark is deeply furrowed, but *Lecanora varia*, a rapid grower, obtains a hold, even on the young branches. The author finds that corticolous lichens are more abundant on sandy than on clayey soil and this is not only, though it may be partly, due to the greater light in the forest, owing to the presence of more birches on the sand. Thus while *Parmelia sulcata* and *P. caperata* require the extra light, *P. physodes*, which is less abundant in woods on clayey than on sandy soils, does not. Hence an undetermined factor correlated with the soil is indicated.

The author gives several observations on the rate of growth of different lichens. The following growths were recorded in one year: *Parmelia physodes* 1.1 cm., 1 cm., *P. fuliginosa* var. *laetevirens* .9 cm., *P. saxatilis* 2.7 cm., *P. caperata* 2.2 cm., *Ramalina calcicaris* 1.5 cm., *Cladonia macilenta* 1.0 cm., *C. fimbriata* .7 cm. These observations showing yearly growth varying from .7 to 2.7 cm. agree very well with those of Bruce Fink (*Mycologia*, 9, pp. 138-158, 1917), who found rates of growth in foliose lichens varying from .3 to 3.5 cm. in a year. The very rapid growth of some lichens depends upon the thallus being of loosely woven texture, as in the case of *Lecidea uliginosa* and *Boeomyces roseus*, the former producing patches 8 ft. by 6 ft. on bare ground during the autumn of 1917. In both these cases, however, the patches were formed by the coalescence of growths from a number of distinct centres of origin. *Cladonia fimbriata*, *C. pyxidata*, *C. floerkiana* and *C. macilenta*, the last two fertile, were observed on rabbit dung.

Harrison, J. W. Heslop. "A Survey of the Lower Tees Marshes and of the reclaimed areas adjoining them." *Trans. Nat. Hist. Soc. Northumberland, Durham and Newcastle-on-Tyne*. New Series, 5, 1918, pp. 89—140, with 7 sketch maps.

The area investigated by the author consists of 14½ square miles of alluvial land lying immediately north of the mouth of the river Tees in the county of Durham, and based on post-glacial sandy clays averaging about 100 feet in thickness, strongly impregnated with calcium and magnesium carbonates washed from the Magnesian Limestone by the streams. These beds were accumulated in the original extensive estuary of the Tees owing to the southern set of the North Sea tides. Much of the estuarine flats so formed was reclaimed in 1740 and again more than a century later by the building of earth and slag sea walls. These cut off long narrow sheets, or "fleets," of largely fresh water, connected by intricate meandering grassy channels called "stells." The area is also intersected by tidal creeks and numerous "lodes" or drains. Further from the sea there are limited areas of undrained and partially drained marsh and fen.

The aquatic stage of the fresh-water marsh or fen succession is poorly developed. In the *Phragmites* reed swamp *Caltha palustris* and *Ficaria verna* are specially prominent before the reed leaves unfold. The mixed marsh or fen association shows the bewildering variety of facies familiar to students of this community. The water, like that of the East Anglian fens, is rich in calcium salts and a very rich flora is present. Local *Saliceta* of various species are found in places. The most interesting species is *Trollius europaeus*, very abundant locally and showing marked differences from the upland form—particularly freer and more luxuriant growth. *Orchis incarnata* and other orchids, with a great number of variants and hybrids, and *Parnassia palustris* are also prominent species. The *Trollius*, which increases and flourishes, reproducing itself freely from seed, where the marsh is a little drier, for instance where the soil is lightened by the action of moles, is suppressed by *Spiraea ulmaria* where these two species meet. The marsh communities gradually pass into meadow with increase of species like *Primula veris*, *Ranunculus acris*, etc., and *Rhinanthus crista-galli*, whose parasitism dwarfs the vegetation.

The largest and deepest fresh-water "fleet" in the reclaimed salt marsh area has a zoned series of communities: first a submerged leaf association of *Myriophyllum spicatum* (d.) and *Potamogeton lucens* (o.), then a reedswamp dominated by *Glyceria aquatica* and *Scirpus maritimus* with *Ranunculus sceleratus* (f.), and *Scirpus lacustris* with *S. maritimus* var. *monostachys* (o.), and finally an open marsh association also locally dominated by *Glyceria aquatica* associated with various *Junci*, *Scirpi* and a few other species. The dry reclaimed area contains no aquatics or salt-marsh plants, and forms a coarse pasture with such grasses as *Holcus lanatus*, *H. mollis*, *Dactylis glomerata*, *Poa pratensis*, *Arrhenatherum elatius*, etc. The accompanying dicotyledonous flora is poor.

True salt-marsh borders the tidal creeks, and besides the primary marsh shows a well-marked secondary marsh formed at a lower level on mud removed from the primary marsh by tidal erosion. "Pans" are very numerous, and according to the author arise from various causes. Of these he considers the most important is the constant presence of standing water. He also agrees with Warming that decaying algae, such as *Fuci*, which have been deposited by the tide in hollows, initiate pans by killing the salt-marsh carpet below. A third cause is the blocking of drainage channels, which may happen in various ways. Suncracks he does not believe initiate pan formation.

The succession of salt-marsh vegetation was followed on various sand and mud spits and banks, and on the silt deposited by specially high tides. *Rhizoclonium*, *Vaucheria* and *Chaetomorpha* are followed by *Salicornia herbacea* or rarely *S. dolichostachya*. Of the glassworts the author found the red form more on the sandy and the "apple-green" form more on the muddy ground, but he concludes, owing to their mosaic mixture over much of the area, that each form is hereditary and that the purple type is heterozygous. *Suaeda maritima* and *Glyceria maritima* follow or sometimes accompany the *Salicorniae*, which include locally *S. ramosissima* and *S. disarticulata*. The mixed *Glyceria-Salicornia* community gives place to an almost pure *Glycerietum*, which in its turn passes to an association dominated by *Glyceria* and *Armeria maritima*, accompanied by *Plantago maritima*, *Festuca rubra*, *Glaux maritima*, *Triglochin maritimum*, *Aster tripolium*, *Artemisia maritima* (at the edge). In newly-colonised muddy hollows *Aster tripolium* followed by *Statice limonium* (ld.) comes into the *Glyceria-Salicornia* stage and this gives a sub-association in which *Spergularia marginata* also occurs. The *Staticetum*, which occupies the main body of the upper marsh and is the stablest of the tidal communities, contains most of the plants hitherto mentioned, with *Spergularia salina* (f.) and *Statice humilis* (vr.), *Glyceria* and *S. limonium* being co-dominant. On levels only covered by the highest spring tides *Armeria* becomes dominant again, and this zone is succeeded by a narrow band of *Artemisia maritima* with local *Obione portulacoides*, and finally by a mixed vegetation of littoral meadow

plants and weeds of cultivated ground. Of these the most noteworthy species are *Bupleurum tenuissimum*, *Cochlearia officinalis* and *Stellaria boreana*. In the secondary marsh formed by debris from the primary thrown down to a lower level *Glyceria* alone survives, forming a turf into which *Statice* and the other accompanying species penetrate as the level is gradually raised above the reach of the majority of tides.

The author distinguishes a submerged leaf association of the saline aquatic formation, inhabiting a large shallow salt-water lake on sandy soil and formed of *Ruppia rostellata* (d.) with *R. spiralis* and *Zostera nana*; and in the pans with permanent salt water *Zannichellia maritima*, *Ranunculus baudotii* var. *marinus*, *Potamogeton pectinatus* var. *salinus*, with the above-mentioned species, occur singly or in pairs. In the sandy salt-marsh succession *Glaux maritima* and *Juncus gerardi* are two of the most important species, while the two liverworts *Aneura pinguis* and *Pallavicinia flotowiana* enter the succession quite early.

Besides the various segregates of herbaceous *Salicorniae* and the *Zannichelliae* and *Ruppiae*, *Statice humilis*, *Salicornia radicans*, *Erythraea pulchella* and *Potamogeton compressus* are new records for the local flora. The two first-named species attain hereabouts the northern limit of their range. A list of *Uredineae* observed has been added as an appendix.

The paper contains a number of interesting and valuable floristic and ecological observations, and it is very greatly to be regretted that the author, owing to war conditions, was unable to make, as he had intended, a really thorough ecological study of the area, not only because it was evidently exceptionally full of interest from both points of view but because we gather it is largely doomed to destruction by industrialisation.

Henry, A. "Woods and Trees of Ireland." *Co. Louth Archaeological Journal*, 1914.

The history of the Irish forests is to some extent shown by the plant remains of the submerged forests and peat mosses. In the former grew Hazel, Alder, Oak, Willow and Pine, whilst in the latter the successive beds seem to indicate a sequence similar to that of the Norwegian Post-Glacial deposits, with *Betula pubescens* in the lowest, Oak in the most recent and a predominance of *Pinus sylvestris* in the intermediate period contemporaneous with Neolithic man.

The high level bogs and those of the western sea-board are regarded by the author as areas which were occupied by forests in the drier and more continental climate of the post-glacial period when the average temperature was probably 4° F. higher than now and when *Pinus sylvestris* inhabited the mountains and western islands now barren of trees. It is pointed out that Labrador with a low average annual temperature (– 4° C.) but a continental climate is well wooded whereas Greenland, which has a higher average temperature (0.5° C.) but an insular climate, is nevertheless treeless. "All tracts covered with furze, bracken, luzula, etc., undoubtedly bore trees till recently; but it is questionable whether the heather-clad moor has borne trees in historic times; while the higher *Eriophorum* and *Scirpus* bogs certainly have not carried forest since the Neolithic epoch."

The incapacity of the Cornish and English Elms to produce fertile seed in this country is regarded as another outcome of the climatic change, since these species reproduce freely by seed in Brittany and Spain respectively; and the absence of Pine, except where planted, from Ireland at the present day is considered to be a further consequence of the altered climate, which eliminated the species from the hills, combined with the effect of cultivation which ousted it from the valleys.

Tetrao urogallus, which is dependent upon the Pine for its winter food, was common at the time of the Conquest but died out about 1760, whilst the tree itself lingered on in Kerry,

Connaught and near Lough Erne till about 1800. As the area of cultivation extended the forests were cleared and extensive exportation of timber hastened their destruction, which was completed, during the latter part of the seventeenth century, by the demands of the iron works.

The following plants and animals are cited as being confined to old woods in Ireland, the relicts of ancient forest:

PLANTS
Cephalanthera ensifolia
Festuca sylvatica
Milium effusum
Monotropa hypopitys
Neottia nidus-avis
Prunus padus
Pyrola media
P. minor
Rhamnus frangula
Stachys betonica

ANIMALS
Mustela martes
Formica rufa
Limax cinerea-nigra
Acanthinula lamellata
Acicula lineata
Hygromia fusca
Pupa anglica
Sphaerodium edentulum
Zonitoides excavatus

These relicts present one or two interesting associations such as the Killarney woods with *Arbutus unedo*, the Oak-Holly association which is common in rocky and hilly districts, and an association of *Quercus robur* and *Ulmus nitens*, such as occupies the banks of the Saône, Adour and Danube. An example of the last-named is found at Abbeyleix.

E. J. S.

Baker, J. G. "The Botany of Burnham Beeches." *Journal of Botany*, 50, 1917, p. 276.

The author here furnishes a list of 176 phanerogams which were noted in this well-known locality during July and August. The area is situated on sandy and gravelly soil and occupies some 374 acres, of which about equal areas exhibit Heath and Woodland vegetation respectively. The flora is of rather a mixed character with a general facies approximating to that of the *Quercetum sessiliflorae*. The dominant trees and shrubs are *Fagus sylvatica*, *Quercus pedunculata*, *Betula alba*, *Ilex aquifolium*, *Crataegus monogyna*, *Calluna vulgaris* and *Erica tetralix*. *Deschampsia flexuosa* and *Molinia coerulea* predominate over large areas but at the same time species occur in abundance which are usually commonest on non-acid soils rich in bases (e.g. *Arum maculatum*, *Galeopsis tetrahit*).

E. J. S.

NOTICES OF PUBLICATIONS ON FOREIGN VEGETATION

Oliver, W. R. B. "The Vegetation and Flora of Lord Howe Island." *Trans. N.Z. Inst.*, 49, 1916, pp. 94-161, and 7 plates.

This is a valuable contribution to the ecology of the outlying islands of New Zealand and Australia, and the author has given a remarkably full account of the flora considering that he spent but fifteen days on the island.

I. *General Introduction.* The physiography is first dealt with. Lord Howe Island has an area of about 13 sq. km., and is situated in S. lat. 31° 32' about 430 km. eastward of Australia. Its rocks are of both volcanic and marine origin. It is mountainous in parts, the highest point mentioned being Mt Gower, 865 m. The climate is distinctly insular. Rainfall is distributed fairly evenly throughout the year, averaging 1818 mm. per annum.

Meteorological tables are included. Reference is made to the animals. The anatomical structure of the leaves of the leading forest trees is discussed and the following points of resemblance noted: (1) Thick cuticle, (2) Aqueous tissue, (3) Dorsiventral arrangement of the mesophyll.

II. *Plant Formations*. These are classified as follows: 1. Woody-Plant Formations (i) Forest, (ii) Moss Forest, (iii) Scrub. 2. Herbaceous Plant Formations (iv) Low Succulent Plants, (v) Sand-Binders, (vi) Rushes, (vii) Tussock Sedges, (viii) Herbaceous Plants. 3. Marine Formations (ix) Mangrove.

(i) *Forest*. A temperate evergreen forest 15-20 m. high occupies the whole of Lord Howe Island except where it is inhibited by adverse climatic or edaphic conditions. High Forest comprises two associations: *Ficus columnaris* and *Acicalyphus fullagari*. Lowland Low Forest comprises the palm *Howea forsteriana* and forest trees such as *Hemicyclia australasica*, *Acronychia baueri*, *Cryptocarya triplinervis*, *Notelaea quadristaminea*, *Lagunaria patersoni*, and *Elaeodendron curtispiculum*. Lianes are abundant and species of ferns, sedges, and herbs occur in open spaces. Mountain Low Forest occurs above 300 m. Here the palm *Hedyscepe canterburyana* is abundant and such trees as *Notelaea quadristaminea*, *Coprosma putida*, *Geniostoma petiolosum*, *Dracophyllum fitzgeraldi*, and *Drimys howeana*. A slight undergrowth of small shrubs and ferns occurs.

(ii) *Moss Forest* occurs on the summits of Mts Gower and Lidgbird. Here the vegetation is of a compact low scrubby nature. Everywhere the ground is covered with mosses. Notable plants are *Dracophyllum fitzgeraldi*, *Clinostigma mooreanum*, *Cyathea brevipinna*.

(iii) *Scrub* occurs at the edge of the forest along the sea coast and on exposed ridges, and consists of shrubs 1-2 m. tall, with a few trailing and herbaceous plants. The coastal scrub association consists of *Ochrosia elliptica*, *Lagunaria patersoni*, *Myoporum insulare*, *Melaleuca ericifolia*, *Carsinia fennifolia*. Hill scrub includes *Dodonaea viscosa*, *Hemicyclia australasica*, *Rapanea platystigma*.

(iv) *Low Succulent Plants* comprise two associations: (a) *Lobelia-Mesembryanthemum*, and (b) *Salicornia*, which occupy coastal rocks and sand within reach of salt spray.

(v) *Sand-Binders* occupy the sand-dunes along the coast and sandy exposed headlands. The association includes *Spinifex hirsutus*, *Ipomaea pescaprae* and *Wedelia uniflora*.

(vi) *Rush Formations* occur on exposed sandy places near the coast. Prominent are *Scirpus nodosus*, *Spinifex hirsutus*, *Poa caespitosa*, *Phragmites communis* and *Ipomaea palmata*.

(vii) *Tussock Sedges* on Talus slopes facing the sea. *Mariscus haematodes* association.

(viii) *Herbaceous Plants* occupy damp ground and dry places not occupied by forest. Associations *Kyllinga monocephala* (damp ground), *Poa caespitosa* (dry ground).

(ix) *Mangrove* occurs on muddy shores between tide marks: *Avicennia officinalis* and *Aegiceras corniculatum*.

The temperate rain forest, except for the absence of gymnosperms, agrees closely in essential characteristics with the rain forests of New Zealand and Tasmania. The moss forest of Mt Gower is similar to that on Sunday Island and on high ground in the North Island of New Zealand.

III. *Origin of the Flora*. The author discusses the geological history of the Island, its possible former land connections, distribution in Australasia of its genera and species, endemism and ecological groups. He comes to the conclusion that "the plants of Lord Howe Island indicate former land connections with both New Zealand and New Caledonia. The greater degree of peculiarity in the New Zealand elements points to the earlier severance of that connection. No closer connection with temperate Australia need be postulated to explain the affinities of the flora of Lord Howe Island and the continent. The last land connection being with New Caledonia, Lord Howe Island ought properly to be considered an outlier of that region."

IV. *List of Indigenous Species.* This is given in full, each species being dealt with under the headings: (a) Recorded, (b) Habitat, (c) Distribution.

The author admits 209 species of vascular plants as indigenous to Lord Howe Island.

V. *Introduced Elements.* A list of thirty introduced plants is given and a short note on the animals.

VI. *Literature and History:* a full bibliography with notes is given.

VII. *Species Omitted.* A short list of species mentioned in former lists but omitted in the present paper forms the conclusion. These species have mainly been confused with others.

C. E. FOWERAKER.

BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING.

The Fourteenth General Meeting (Fifth Annual Meeting) was held on December 21st in the Botanical Lecture Room, University College, London, the President of the Society, Dr W. G. Smith, occupying the Chair. After the usual formal business the report of the Hon. Secretary was read and adopted.

HON. SECRETARY'S REPORT FOR 1918.

Most Societies in the period of stress of the past four years have had to deplore a decrease in their activities consequent not merely on the difficulties of arranging meetings but also on the many and exacting occupations which have prevented members from attending. It is therefore a matter of no little satisfaction that during the past year the various activities of the Society have augmented rather than decreased. All will, we venture to think, agree that the JOURNAL OF ECOLOGY has maintained its high reputation, whilst in place of the two meetings usually held it was found possible to arrange three during the past season. The two Field Meetings, namely, a one-day excursion to Breckland and a five-days' meeting at Settle, may both be characterised as unqualified successes, and the number of members present on each occasion was, under the circumstances, particularly gratifying. The Meeting at Settle which was held in conjunction with the Yorkshire Naturalists' Union is, we trust, but the prelude to further such happy co-operative efforts. The thanks of the Society are due to Dr Woodhead and Mr Cheetham and also to Dr Farrow, who were responsible for the programmes of the two Field Meetings respectively, and to whom we largely owe their success. In respect to the membership it could hardly be expected that this would show any considerable increase, but it is a sign of the widespread appreciation of the work of the Society that six new members have joined the Society, and further that the additional members are not from this country alone but represent such widely separated regions as Italy, New Zealand and the United States.

We have to lament the loss of two members by death in the past year, Dr Ethel Sargant and Dr Ethel de Fraine. The Hon. Secretary has received one resignation, so that the membership compared with that of 1917 shows a net increase of three, bringing our total to 114.¹

¹ Since this report was read 3 further resignations have been received and 4 more members have joined the Society to April 1, 1919 (see list of members, p. 117).

INCOME AND EXPENDITURE FOR THE YEAR 1917

<i>Income</i>		<i>Expenditure</i>	
	£ s. d.		£ s. d.
Subscriptions received ...	99 0 0	<i>Journal of Ecology</i> —Cost for 1917 ...	221 13 11
Do to receive ...	3 3 0	Postages and Sundries—Secretary ...	3 14 7
Do prepaid ...	6 6 0	Balance—Surplus on the year, carried to	33 2 2
	108 9 0	Balance Sheet below
Written off ...	4 4 0		
British Vegetation Committee. Share of profits on sales of <i>Types of British Vegetation</i> ...	104 5 0		
<i>Journal of Ecology</i> —Sales ...	6 13 8		
	147 12 0		
	258 10 8		258 10 8

BALANCE SHEET AT 31st DECEMBER, 1917

<i>Liabilities</i>		<i>Assets</i>	
	£ s. d.		£ s. d.
Subscriptions prepaid ...	6 6 0	<i>Journal of Ecology</i> —Balance due from Publishers ...	27 2 0
Balance—Surplus brought forward from 31st Dec., 1916 ...	2 1 9	Cash at London, County and Westminster Bank ...	11 4 11
Surplus on year 1917, as above ...	33 2 2	Outstanding Subscriptions to receive ...	3 3 0
	35 3 11		
	41 9 11		41 9 11

NOTE. The unsold stock of the *Journal of Ecology* is a further asset.

HUGH BOYD WATT,
Hon. Treasurer.

I have examined the accounts for the year ended Dec. 31st, 1917, and certify them to be a correct statement and that all vouchers are in accordance with receipts and payments shown therein.

CHAS. OLDHAM.

November 22nd, 1918.

HON. TREASURER'S REPORT.

In presenting the audited accounts for 1917 (p. 109) the Hon. Treasurer, Mr H. B. Watt, stated that the Society might consider its financial position very satisfactory, especially considering the war conditions that had prevailed. In seconding the motion for the adoption of the accounts, Mr Tansley said that the JOURNAL for 1918 had been rather larger than was strictly justified by the funds available, the cost of production having risen considerably during the year. In 1919 it would be prudent to publish only two issues of ninety-six pages each. The accounts were adopted without a dissentient.

The meeting then proceeded to the election of Officers and Council Members for the ensuing year. The following were unanimously elected: Vice-President, R. Lloyd Praeger; Hon. Editor, A. G. Tansley; Hon. Secretary, E. J. Salisbury; New Members of Council, W. E. Brenchley, O. V. Darbishire, F. W. Oliver, W. Watson.

PRESIDENT'S ADDRESS

The President (Dr W. G. Smith) then delivered his address and spoke as follows:—

This is a memorable meeting. The end of the Great War is in sight and we stand on a threshold. Behind is a darker period when problems in plant ecology and such-like appeared trivial beside the greater issues, and when one's thoughts constantly turned towards the trenches, the battery positions and the North Sea. The outlook is still obscure but we feel we must be up and doing.

The predominant feeling at the beginning of the war was one of resentment and sorrow that one of our aims as a Society was shattered for the time being. For years there had been a movement towards the elimination of racial differences and the fostering of one community of botanists. The International Association of Botanists, the British Association, and the I.P.E. had carried us beyond a merely literary connection to a social one and even to comradeship in the field. In Britain, as in Europe and North America, recognition as a botanist was a universal credential, and the reception many of us have met with in different parts of the world was almost overwhelmingly friendly and hospitable.

It was a rude awakening to find that politics and diplomacy had made enemies of many with whom, in spite of all, we can never quite lose the tie of comradeship. It has been a tragedy of the war that Belgium, the sphere of many international excursions, should be the chief cock-pit. Some of us can recall the places themselves, whilst the topography and botany were familiar from a wide literature culminating in the vivid monographs of Jean Massart. As the tide of war swept backwards and forwards, one could not help thinking of the wrecked labours of the peasants of Belgium and Picardy who by intensive effort had built up a great soil fertility round the numerous villages. Thus there arises a feeling, political, economic and ecological, which finds expression in the title page of Massart's *Pour la Protection de la Nature en Belgique*. It is probable that in our narrower sphere as a Society we may be asked to do something towards replacing some of this damage, and by a ready response we shall best show sympathy.

The darker side has also been impressed on us as a Society which has constantly fostered the younger men. We have missed their energy in the more exacting field surveys, their presence at the meetings, and their contributions to the JOURNAL. It is therefore natural that we should count our losses and think what might have been done by such men as C. Laidlaw, E. Lee, A. S. Marsh and D. Macpherson. What applies in our own Society can be extended to all spheres that have paid toll in the younger men who have given all they could give. It is significant that since the last President's Address the Society has lost by

death three eminent women—Dr Sarah M. Baker, Dr Ethel de Fraine, and Dr Ethel Sargent. The Society has always maintained equality of the sexes and has gained thereby the cooperation of very active workers. Each of those just named has left knowledge more complete than she found it, and no worker wishes a better epitaph. Their distinction is a measure of the loss of the Society, and the personal loss is deeply felt by members.

ECONOMIC PLANT ECOLOGY.

The war years have revealed many national needs. One of these is the application of science to industry. In the past there has been a serious lack of unity between what is commonly called science and practice. As botanists we have tended to be academic, though some have broken away from the narrower sphere. That economic problems in plant life are important these years have made evident, but it is stimulating to find that plant ecology has taken a forward position in economic applications¹. The future has a strong call for the younger generation to develop this wider economic aspect, because the older race do not so easily shake off acquired habits of thought and action. But in adopting the economic outlook, do not let us despise the more scientific. It may be said, almost without exception, that the more pressing problems in applied botany lie along the imperfectly explored fringe of the territory. In other words, applied problems call for a thorough scientific foundation and a broad mental equipment. Plant nutrition will be chaos until we know more about controlled plant cultures, leaf activities, synthesis of carbohydrates and the phenomena of absorption. Hybridisation will not be solved by Mendel's principles alone, but by something which still lies in the future. Soil biology is still very much a collection of detached observations. As with these, so with plant ecology, the problems must be attacked from the foundation in the spirit of scientific research and without any immediate "practical objective."

Another aspect of applied science should not be overlooked. It is needful to find out what are the urgent problems. This exploration can only be done by going into the territory where the problems exist, and it means that the ecological botanist must become familiar with the economic side by primary surveys of various kinds. In doing this it is above all necessary to approach the subject free from bias and unfettered by any dogmatic general opinion.

PLANT COMMUNITIES AND BIOLOGICAL FACTORS.

Plant ecology has many tempting vistas for a Presidential Address. In some respects ecology is a modern edifice, yet the crudeness has its advantages, there is no long trail of accumulated facts trodden into a hard road polished with empiric formulae. There is still an opportunity to muster our facts and if need be to re-cast our theories.

The foundation of Plant Ecology is that the plant and its community are the true index of the environment, and that a change in the community must be accounted for by the action of factors of the environment. The tendency of the earlier work, especially in primary survey, was to seek the determining factors amongst the climatic and edaphic conditions. It would be an interesting survey to trace the gradual improvement in the methods of observing and recording these factors. A perusal of the volumes of the *Journal of Ecology* will show that in spite of many difficulties there is a progressive adaptation of the methods of the laboratory to the requirements of outdoor observation and experiment.

Another noteworthy evolution is the increasing reference to biological agents. There was a distinct tendency in the earlier work to turn the blind eye towards the biological factors. It was also considered a strong argument in destructive criticism to point out that Britain was so much under the influence of Man and his activities that environmental studies were impossible and useless. This argument is a fallacy. It could be applied to

¹ Carey, A. E. and Oliver, F. W., *Tidal Lands*, 1918.

all Europe and to much of the United States, which may claim to be cradles of modern plant ecology. That Britain is not unduly influenced by man is emphasised by several of the botanists who spent five weeks in all parts of Britain with the I.P.E. in 1911. Professor C. Schröter with a long and thorough knowledge of Swiss and other European vegetation says—"So sehen wir zu unserem Erstaunen in dem dichtbevölkerten England enorme Strecken extensiv oder gar nicht bewirtschafteten Bodens, in starkem Gegensatz zu der intensiven Bodenbenutzung unseres schweizerischer Mittellandes¹." Professor Jean Massart of Brussels refers to—"L'étendue des espaces qui sont laissés incultes pour le gibier²." Professor H. C. Cowles (Chicago)—"I was amazed at the vast amount of wild country in densely populated England³." To reverse the argument—where is the influence of man on the vegetation not perceptible? In South Africa, the influence of man, including veld burning and stock grazing, has had a great effect in changing the composition of the Veld and in limiting the extension of bush⁴. In New Zealand there has been wide dispersal of imported weeds, and where stock graze the native plants are restricted to rocks and places inaccessible to grazing animals⁵. Still further south, Campbell Island (lat. 52° 35' S.), is a sheep farm, and on Lord Auckland's Islands (lat. 50° 30' S.) pigs, introduced in 1807, have multiplied and have influenced the vegetation⁶.

The recognition of biological factors is the more necessary because the economic applications of plant ecology are closely linked with the biological environment. The present position is that a certain number of observations have been recorded, but much remains to be tested by controlled experiment. At such an early stage it is perhaps hazardous to lay down principles, but it may be of assistance to ecologists if an attempt is made to formulate some concepts.

I. Biological factors play a part in the environment of every type of vegetation, both natural and semi-natural. Insects in pollination and in finding food may modify the occurrence of a plant species or community. Another wide sphere for the operations of organisms is involved in the term soil-biology. The interaction of plants in a community, and of one community with another may also be included under biological factors. Herbivorous animals exist wherever there is vegetation, and by grazing they influence the whole vegetation or modify the plant communities. When man comes in, his activities as farmer, grazier and hunter bring fundamental changes. It is unnecessary to attempt an exhaustive list, because it is evident from the indications just given that the present state of knowledge is very imperfect. A wide field still lies open for exploration, and while searching for new facts, observers will do well to examine critically what is accepted as old, but which has not been tested by controlled experiment.

II. The effects of biological factors may be continuous or discontinuous either in time or space. Some biological factors have little real significance, for instance an insect attack limited in area and lasting only a season; or the burning of some plant community as an accidental occurrence. These might be important in the study of a restricted locality, but in dealing with larger areas they must be regarded as local episodes. At the other extreme there are biological factors that are more continuous in their effects than many edaphic conditions, e.g. fluctuations in moisture due to wet and dry seasons. Grazing on the large scale in stock-farming is a continuous factor and varies little from year to year if directed

¹ *New Phytologist*, **11**, No. 8, p. 282, October, 1912.

² *Idem*, No. 1, p. 27, January, 1912.

³ *Idem*, p. 26.

⁴ *Bews, J. W.*, *The Grasses and Grasslands of S. Africa*, 1918.

⁵ *Ashton, B. C.*, "Some Effects of Imported Animals on the Indigenous Vegetation." *Proc. New Zealand Inst.* **44**, 1912.

⁶ *Cockayne, L.*, "Botanical Excursion to the Southern Islands." *Proc. New Zealand Inst.* 1904.

by the same occupier. The stock wintered on a sheep farm is almost the same each year, and the allocation of the land to each flock-unit remains the same. Drainage is another factor which cannot change much from year to year, though there is a slow change if the drainage system is not maintained, and this becomes evident on the herbage. Moor-burning will be a continuous factor if carried out regularly. Considerable discretion is necessary in estimating the importance of any environmental factor. It would be wrong to give undue prominence to some localised agent (except in a local study of vegetation) and to apply this activity to wide areas which have not been examined sufficiently. On the other hand, one need not be unduly disturbed because one finds considerable variation in the treatment of one grazing farm from another. If one attempts to distinguish all the variations that exist, then the survey becomes a record of the merits or deficiencies of individual occupiers, and this might lead to awkward results. In classifying grasslands the case will generally be met by some unit comparable to the species in taxonomy, though for more detailed work it may be necessary to define varieties of the species.

III. The effect of biological factors is to reduce the growth-forms from phanerophytes to chamaephytes and ultimately to hemicyptophytes. These terms were originally used by Raunkiaer to designate zones influenced by climate, but they are appropriate here because the protection of the buds is fundamental as regards biological factors. Forest when destroyed by axe or fire is replaced by scrub, and continues as such if these biological agencies are recurrent. Trees and scrub-plants are further repressed by grazing animals (including rabbits). During the seedling and younger stages of the plants, the buds are exposed at some distance above the surface of the soil, and are liable to removal; again, in trees and shrubs the possibilities of bud-production in the axils of cotyledons and lower leaves are limited. Scrub-plants like *Ulex* and *Crataegus* are more persistent because, although grazed as young plants, there is abundant bud-production near the soil level; spines also afford some protection to the older plants. The same applies to *Rosa* and *Rubus* scrub, since renewal is largely from buds formed at or near the soil-level. Chamaephytes are represented in Britain mainly by Callunetum, Vaccinietum, and heath types with Ericaceae and Vaccinia. While these mainly represent climatic and edaphic conditions unfavourable to tree growth, one is compelled in many cases to refer them to biological factors. Heath plants return again after periodic burning, and they resist grazing: *Vaccinium* because of numerous reserve buds below the soil-surface; Ericaceae and *Empetrum* because the seedling leaves are closely crowded near the soil and each has a potential axillary bud.

Grassland is much the most common stratum of vegetation that results from biological factors. Encroachment of grassland on forest is a dominant topic in all text-books on plant ecology, and it is to a great extent the result of biological factors; veld-burning in South Africa, and prairie-burning in North America are notable examples¹. Where the forest has been cleared and cultivated, the land remains arable so long as the plough remains operative, but in almost every case grassland follows if ploughing ceases. Common to forest, scrub and Callunetum there is a system of grass invasion along the zone marginal to streams and springs. Periodic erosion, deposition and flooding promote conditions favourable to open plant communities, from those on recent shingle to those forming the earlier stages of the reed swamp. Grassland follows naturally, sooner or later, and once established it is maintained and extended by grazing animals. The stream system thus affords numerous points of attack on the forest and moorland, and the breaches made are maintained and extended wherever grazing animals have access. If man appears as a cultivator he tends to follow the larger valleys so that encroachment proceeds faster. Man also curtails the opener communities of the marginal belt of swamp and marsh, by

¹ Cf. Clements, F. E., "Plant Succession," 1916, *Prairie-Plains Climax*, etc.

embanking the rivers, and thus produces fen grassland much safer and more useful for his grazing stock¹.

The limiting of natural factors by biological agents might also be followed out for salt marsh, sand dune and shingle beach². The result is strikingly similar for forest, moor, river system or maritime vegetation: if a grassland phase appears it is encouraged and developed by grazing animals and the influence of man. The development of grassland is thus convergent from several sources. This diverse origin may not be significant when grassland is regarded as a collective unit (Schimper, Warming, etc.), but when subdivision is required the problem of origin becomes important.

Our present purpose does not require a comprehensive scheme of classification of grasslands³. There is a general agreement that some grasslands are natural, others are semi-natural. The natural types have never been ploughed or systematically manured. Semi-natural grassland has been ploughed and allowed to revert; Stapledon divides them into untended and tended. It is also assumed that, whether resulting from natural colonisation or from artificial sowing, grassland attains in a few years to a relatively stable condition if maintained under a uniform system of mowing, grazing, manuring, etc. These larger groups of grassland include subdivisions representing evolution in response to variations in edaphic and biological conditions; the extremities of the series may be distinguished as moist versus dry, and richer versus poorer soils. Throughout them all, certain species of grasses appear again and again, so that distinctions between grassland communities are based mainly on the relative frequency of a limited number of grasses, and on the presence or absence of other flowering plants.

WHY SOME GRASSES ARE WIDELY DISTRIBUTED.

If, for the present, attention is limited to the British or "Atlantic-type" of grasslands, and to the grasses, excluding other plants, then it seems possible to select factors which will eliminate locally distributed species, and leave a residue of grasses common to most types of grassland. The results have been arrived at by applying to British grasses the facts relating to their morphology and ecology, collected by C. Raunkiaer, Stebler and Schröter, Volkart, etc.

(A) The dominant grasses are perennials, that is species which produce a limited number of flowering shoots and a larger proportion of leafy shoots each year. If from a British Flora a list is made of the annual (monocarpic) grasses, it will be found to include mainly the locally occurring species. Yet there are notable exceptions: *Poa annua* is widespread, but it may form a permanent turf (as in many lawns) if it is constantly mowed or grazed, and it is also distinguished by its winter-greenness; *Bromus mollis* and *B. race-*

¹ The contrast between the "unharnessed" Danubian "Plav" and the cribbed and controlled Norfolk Broads is seen in the descriptions by Miss M. Pallis: "Types of British Vegetation," *The River-Valleys of East Norfolk*, Chap. x. Cambridge, 1911. "Structure and History of Plav," *Journ. of Linnean Soc.—Botany*, 43, July, 1916.

² Cf. this JOURNAL, papers on Blakeney Point by Oliver, F. W., etc.; "The Salt Marshes of the Dovey Estuary," by Yapp, R. H., Jones, O. T. and Johns, D., 5, 1917.

³ The basis of such a classification is outlined in the Swiss "Wiesen" memoirs of Stebler and Schröter. For British grasslands, lists from various representative grasslands are given in "Types of British Vegetation." From the agricultural side, many lists have been published, including the classic series of analyses from the Rothamsted Experiment Station. The more recent papers in the *Journal of Agricultural Science* (Cambridge) are useful for reference; Armstrong, S. F., "Botanical and Chemical Composition of the Herbage of Pastures and Meadows" (20 analyses from Leicestershire, Northants, etc.), 2, 1907-8; Stapledon, R. G., "Pasture Problems," 5, 6, 8, etc.

mosus are not uncommon in hay meadows where they flower and shed seed before other grasses, and the seedlings find a place in the open turf so often found in newly cut meadows; they are also very winter-green.

(B) Common grasses possess a high power of shoot production from buds near or below the surface of the soil. This property brings about quick renewal after grazing, and it favours grasses in competition with trees and shrubs with few and exposed buds. The grasses which form loose tufts, because they have decumbent stems with many nodes, have a structure favourable for bud-development, and most of the commoner grasses are loose-tufted. Long subterranean runners with many scale-leaves would appear to present opportunity for bud-production, but grasses like *Ammophila* on sand, *Phragmites* and *Glyceria* on mud, and *Agropyrum repens* are more frequent as colonisers than as elements in permanent grassland. *Bromus erectus* is another exception; though apparently well adapted, it does not withstand close grazing.

(C) A high power of surviving critical periods, especially winter and drought:

Winter resistance. In Britain some grasses continue fresh and green throughout the winter. There may be a check because of low temperature or snow, but there is a fairly continuous production of shoots. During milder weeks, a sward of grass bitten by frost or bleached by snow soon recovers its fresh green. These winter-grasses thus maintain any ground occupied, and in spring they extend into spaces in the sward left vacant by less active species. By combining observations with records by Raunkiaer¹ and Volkart², the grasses may be grouped according to winter-greenness:

Winter-green³:

<i>Poa trivialis</i>	<i>Lolium perenne</i>
<i>P. compressa</i>	<i>Cynosurus cristatus</i>
<i>P. pratensis</i>	<i>Holcus lanatus</i>
<i>P. annua</i>	<i>Bromus mollis</i>
<i>Alopecurus</i> spp.	<i>Avena elatior</i>
<i>Festuca ovina</i> (agg.)	<i>A. flavescens</i>
<i>F. gigantea</i>	<i>A. pratensis</i> (1)
<i>Dactylis glomerata</i>	<i>Deschampsia caespitosa</i>
<i>Bromus erectus</i> (2)	<i>Agrostis alba</i>
<i>Ammophila arenaria</i> (7)	<i>Hordeum pratense</i> (3)

Winter-green in a less degree (young leaves concealed during winter by bleached leaves):

<i>Agrostis vulgaris</i>	<i>Holcus mollis</i>
<i>Anthoxanthum odoratum</i>	<i>Phleum pratense</i>
<i>Koeleria cristata</i> (4)	<i>Briza media</i> (6)
<i>Glyceria fluitans</i>	<i>Hordeum silvaticum</i> (5)
<i>Elymus arenarius</i> (7)	<i>Nardus stricta</i> (8)
<i>Sesleria coerulea</i> (9)	<i>Festuca pratensis</i> (10)

Less winter-green (lose leaves early and recover late in spring):

<i>Glyceria aquatica</i>	<i>Bromus inermis</i>
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Majority of woodland grasses

¹ Raunkiaer, C., *De Danske Blomsterplanter Naturhistorie*, 1, Copenhagen, 1895-99.

² Volkart, A., "Gramineae" in *Lebensgeschichte der Blütenpflanzen Mitteleuropas*. Bd. 1, Abt. 2. Stuttgart, 1908.

³ The grasses to which numbers are affixed, although winter-green, are restricted in distribution: (1) Highland and upland alluvials; (2) chalk and limestone; (3) local on moist grasslands; (4) fixed dunes and mountain limestone; (5) calcareous and Permian scrub; (6) frequent, but rarely gregarious; (7) dunes; (8) peat and clay, poor soils; (9) mountain limestone, and calcareous scars; (10) uncommon in old northern grassland, though often sown.

Summer-green:

Brachypodium pinnatum
B. sylvaticum

Phalaris arundinacea
Hierochloe odorata

Deciduous leaves:

Molinia coerulea

Phragmites communis

The groups from "less winter-green" onwards consist of grasses which do not occur in the more widely distributed grasslands. The "winter-green" groups include all the commoner grasses along with others which are local in habitat, as indicated.

Drought resistance. The short but not infrequent periods of drought in Britain have a marked effect on the pastures and some grasses are influenced more than others. That there is a process of elimination is evident from the only detailed study of this aspect known to me¹. This is a study of herbage already sorted out so that the competition is between plants more or less equally adapted to drought. A period of summer drought introduces a sequence. The drought causes certain species to disappear (e.g. *Poa trivialis*, *Cynosurus cristatus*, *Avena flavescens*, White Clover, etc.), while others persist (*Lolium perenne*, *Dactylis*, *Bromus erectus*, *Agrostis vulgaris*, *Lotus corniculatus*, etc.). Colonisation of ground left unoccupied takes place by Buttercup, Daisy, Yarrow, etc. The return of moister conditions induces recovery of ousted species; some recover before winter (*Agrostis stolonifera*, *Poa pratensis*, *P. trivialis*, *Trifolium* spp., etc.), others do not recover till spring (*Festuca pratensis*, *Holcus lanatus*, *Cynosurus*, *Phleum*, etc.).

(D) Adaptability to habitat is a feature of common grasses. What this means is distinctly vague, but its application is seen when it is considered that grasses apparently adapted to be widespread are restricted in distribution. These are generally colonisers—*Ammophila* and *Elymus* on sand, *Glyceria maritima* on salt marsh, *Glyceria fluitans* on mud alluvials, *Sesleria* on limestone, etc. In each there is a limiting factor which dominates perennialness, abundance of dormant buds, and winter-greenness. Just as an intricate key will only unlock a particular combination, so these grasses fit a limited habitat. The commoner grasses are more like a master-key, and fit a whole series of combinations which appear to be different, judged by the standards at our disposal.

In conclusion, I have claimed the privilege of the Presidential Address to cover a wide range of topics, to suggest rather than to explain, and to allow accumulated experience to express itself. If an impression is left that there is much work still to be done on biological factors, then one purpose is served. On the other hand, it is to be hoped that the attempt to make a consecutive chain has not failed. There is evidence that detailed Morphology can throw light on the evolution of a community of grasses, but much remains to be done before we can clear up the obscurity of terms like "resistance to winter" and "adaptation to habitat."

On the proposition of Prof. Oliver seconded by Mr Tansley a hearty vote of thanks was accorded the President for his Address.

Prof. Oliver then dealt with the Grasses of Waste Lands and their exploitation for paper making. Samples were exhibited of paper made from *Spartina townsendii*, *Agropyrum repens*, *Ammophila arenaria* and *Phragmites communis*. The meeting concluded with an exhibition by the Hon. Secretary of a draft scheme for the Black and White representation of Vegetation depending on the use of a basis symbol for the various associations of a type of vegetation such as forest, moor, etc.

E. J. SALISBURY,

Hon. Sec.

¹ Stapledon, R. G., *Journ. Agric. Science*, 5, 1912-13. See Abstract, this JOURNAL, 1, p. 197, 1913.

LIST OF MEMBERS (APRIL 1ST, 1919)

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, Dr E. J. SALISBURY, The Briars, Crosspath, Radlett, Herts.

Accessions Dept. Library, Columbia University, New York.

Adamson, R. S., M.A.; Botanical Dept., University, Manchester.

Aimer, James; Technical School, Bell Street, Dundee.

Allorge, Pierre; Laboratoire de Botanique, Sorbonne, Paris.

Andersonian Naturalists' Society (*Secretary*, **H. G. Cumming**, 90, Barrington Drive, Glasgow).

Armitage, Miss E.; Dadnor, Ross, Herefordshire.

Bews, Prof. J. W.; University College, Pietermaritzburg, Natal, S. Africa.

Birt, Miss E.; 22, Denmark Terrace, Brighton.

Blackman, Prof. V. H., F.R.S.; Imperial College of Science, London, S.W. 7.

Blackwell, Miss E. M., M.Sc.; 16, Stanley Avenue, Birkdale, Southport.

Blatter, Father E.; St Xavier's College, Bombay.

Bloomer, H. H.; Cottesloe, Featherstone Road, Streatley, Sutton Coldfield.

Bolland, B. G. C.; Department of Agriculture, Cairo, Egypt.

Bournemouth Natural History Society (*The Librarian*, Municipal College, Lansdown, Bournemouth).

Brenchley, Dr Winifred E.; Rothamsted Experiment Station, Harpenden, Herts.

Brennan, A.; Technical College, Newport, Mon.

Brooks, F. T., M.A.; Botany School, Cambridge.

Brown, George, M.A.; School House, Littlemill, Patna, Ayrshire.

Bureau of Science (*Librarian*), Manila, Philippine Islands.

Carter, H. G., M.B.; Royal Botanic Gardens, Calcutta.

Cavers, Dr F.; 49, Hamilton Road, London, N. 5, *Hon. Life Member*.

Chipp, T. F.; Assistant Director Botanic Gardens, Singapore.

Clarke, Dr Lilian; James Allen Girls' School, E. Dulwich Grove, London, S.E. 22.

Cockayne, Dr L., F.R.S.; Ngaio, Wellington, New Zealand.

Cotton, A. D.; Herbarium, Royal Gardens, Kew.

Croydon Natural History and Scientific Society (Miss **Grace Bigby**, 15, Stonehill Mansions, Streatham Hill).

Crump, W. B., M.A.; The Lodge, Rastrick, Brighouse, Yorks.

Cutting, E. M., M.A., B.Sc.; 125, Tredegar Street, Bow, London, E.

Darbishire, Dr Otto V.; Botanical Dept., University, Bristol.

Delf, Dr E. M.; Westfield College, Hampstead, London, N.W.

Dewar, Dr J. M.; 5, Chalmers Street, Edinburgh.

Drabble, Dr Eric; 13, Claverley Grove, Church End, Finchley, London, N.

Dymes, T. A.; Carthona, West Drayton, Middlesex.

Essex Field Club, The (Essex Museum of Natural History, Romford Road, Stratford, Essex).

Farmer, Prof. J. B., F.R.S.; Imperial College of Science, London, S.W. 7

- Farrow**, Dr E. P.; Limehurst, Spalding, Lincs.
- Fritsch**, Prof. F. E.; East London College, Mile End Road, E. 1.
- Fyson**, P. F.; The Presidency College, Madras, India.
- Gordon**, G. P., B.Sc.; West of Scotland Agricultural College, Blythswood Square, Glasgow.
- Halket**, Miss A. C., B.Sc.; Bedford College, Regent's Park, London.
- Hampstead Scientific Society** (*Librarian*, 92, Fellows Road, Hampstead, N.W.).
- Hartshorn**, John; School House, Leyburn S.O., Yorkshire.
- Henkel**, J. S.; Conservator of Forests, Pietermaritzburg, S. Africa.
- Hill**, T. G.; 9, Bloomfield Terrace, Pimlico, London, S.W.
- Howarth**, W. O.; 61, Cecil Park, Crouch End, London, N. 8.
- Hume**, Miss E. M. M.; 57, Doughty Street, London, W.C. 1.
- Jefferies**, Rev. T. A.; 324, Mansfield Road, Nottingham.
- Jeffreys**, H., M.A., D.Sc.; 199, Albany Street, Regent's Park, London, N.W. 1.
- Jenkin**, T. J., B.Sc.; University College, Bangor, N. Wales.
- Johns**, D., B.Sc.; County Education Office, Carmarthen, S. Wales.
- Johnson**, Miss Edith; 63, Oriel Road, North End, Portsmouth.
- Johnson**, Prof. J. C.; University College, Auckland, New Zealand.
- Johnstone**, Miss Mary; 43, Hill Top Avenue, Cheadle Hulme, Cheshire.
- Jones**, Miss G. M.; The Cottage, Wraysbury, Wilts.
- Laurie**, Miss C.; 1, Vittoria Walk, Cheltenham.
- Leah**, Miss A.; 23, Scarborough Road, Shipley, Yorks.
- Macgregor**, M.; 33, George Square, Edinburgh.
- McLean**, Dr R. C.; Duart, Holmes Road, Reading.
- Mangham**, S., M.A.; Armstrong College, Newcastle-on-Tyne.
- Matthews**, J. R., M.A.; Birkbeck College, London, W.C.
- Morey**, F.; Wolverton, Carisbrooke Road, Newport, Isle of Wight.
- Morris**, George, B.Sc.; Friends' School, Saffron Walden, Essex.
- Moss**, Dr C. E.; University of South Africa, Johannesburg, Transvaal.
- Negri**, Dr Giovanni; R. Instituto Botanico, Torino, Italy.
- Newman**, Leslie F., M.A.; School of Agriculture, Cambridge.
- Nicholson**, C.; 35, The Avenue, Hale End, Chingford, E. 4.
- Nimmy**, E. W.; 210, Whippendell Road, Watford, Herts.
- Oakley**, W. J.; 20, Head Street, Halstead, Essex.
- Oldham**, Charles; The Bollin, Shrublands Road, Berkhamsted, Herts.
- Oliver**, Prof. F. W., F.R.S.; University College, London, W.C.
- Oliver**, W. R. B.; 5th Avenue, Tauranga, New Zealand.
- Orr**, M. Y.; Royal Botanic Gardens, Edinburgh.
- Osborn**, Prof. A. H.; University of Adelaide, Australia.
- Pammell**, Prof. L. H.; Iowa State College, Ames, Iowa, U.S.A.
- Paulson**, R.; Glenroy, Cecil Park, Pinner, Middlesex.
- Pearsall**, W. H., M.Sc.; Ivy Dene, Dalton in Furness, Cumberland.
- Pearse**, Miss Eleanor; 3, Bessborough Mansions, Vauxhall Bridge Road, London, S.W.
- Pearson**, A. A.; Gatcombe House, Oatlands Avenue, Weybridge.
- Porter**, Mrs, B.Sc.; Lehenagh House, Cork, Ireland.
- Praeger**, R. Lloyd; National Library, Kildare Street, Dublin, *Vice-President*.
- Price**, S. R., M.A.; Botany School, Cambridge.
- Quick**, B. E.; Lowell, Michigan, U.S.A.
- Radley**, L. W.; 8, Croxted Road, Dulwich, London, S.E. 21.
- Ramsbottom**, J., M.A.; Botanical Dept., Natural History Museum, London, S.W.
- Randell**, Miss F. A.; 37, Temple Street, Oxford.

- Rayner**, Dr M. C.; University of London Club, 21, Gower Street, W.C. 1.
Rübel, Dr E.; Zürichbergstrasse 30, Zürich, Switzerland.
Salisbury, Dr E. J.; The Briars, Crosspath, Radlett, Herts, *Hon. Secretary*.
Shelford, Prof. Victor E.; 506, W. Iowa Street, Urbana, Illinois, U.S.A.
Skene, Macgregor, B.Sc.; Avondow, Milltimber, Aberdeen.
Smith, Dr William G.; 9, Braidburn Crescent, Edinburgh, *Hon. Life Member, President*.
Smith, Miss Winifred; 3, Endsleigh Gardens, London, N.W. 1.
Stapf, Dr O., F.R.S.; Herbarium, Royal Botanic Gardens, Kew.
Stapledon, R. G., M.A.; University College, Aberystwyth.
Stevenson, Miss E. H.; 28, Foxcombe Road, Weston, Bath.
Stiles, W., M.A.; 35, Rylett Road, Shepherd's Bush, London, W. 12.
Sutherland, Prof. G. K.; Sunnybank, Manlocky, Ross-shire.
Tansley, A. G., F.R.S.; Grantchester, Cambridge, *Hon. Editor of the Journal*.
Taylor, Norman; Brooklyn Botanic Garden, Brooklyn, N.Y., U.S.A.
Thoday, Prof. D., M.A.; S. African College, Cape Town, S. Africa.
Trow, Prof. A. H., D.Sc.; 50, Clive Place, Penarth, Glamorgan.
Vines, Prof. S. H., F.R.S.; Botanic Garden, Oxford.
Waterfall, C., F.L.S.; Dalmeny, Shavington Road, Chester.
Watson, W., D.Sc.; Taunton School, Taunton, Somerset.
Watt, Hugh Boyd; 12, Gt James St, Bedford Row, W.C. 1, *Hon. Treasurer*.
Weiss, Prof. F. E., F.R.S.; University, Manchester.
Wells, Dr Morris M.; Dept. of Zoology, University of Chicago, Chicago, Illinois, U.S.A.
Willan, G. R.; Glan-yr-Afon, Cefn Coed, Merthyr Tydfil, S. Wales.
Williams, Miss W.; 68, Trinity Street, Barry.
Williams, Prof. Lloyd; University College, Aberystwyth.
Wills, Miss Lucy; 57, Doughty Street, London, W.C. 1.
Wilmott, A. J., M.A.; Botanical Dept., Natural History Museum, London, S.W.
Woodhead, Dr T. W.; Technical College, Huddersfield, Yorks.
Woodruffe-Peacock, Rev. E. A.; Cadney Vicarage, Brigg, Lincs.
Wortham, Miss W. H.; The High School, Kendal.
Yapp, Prof. R. H., M.A.; Queen's University, Belfast, Ireland, *Vice-President*.
Yorkshire Naturalists Union (**C. A. Cheetham**; Stonebridge Mills, Wortley, Leeds).

THE ECOLOGICAL SOCIETY OF AMERICA

The annual meeting was held at Baltimore, December 26 to 28, 1918, under the presidency of Professor Henry C. Cowles, of Chicago, who delivered an address on "Ecology in Reconstruction." The committees on Climatic Conditions, the Preservation of Natural Conditions for Ecological Study, Freshwater Fish and Fisheries, and Soil Temperatures reported.

Abstracts of a few of the papers read are subjoined.

Cowles, H. C., University of Chicago. "The Illinois Forestry Survey."

The Department of Registration and Education of the State of Illinois has undertaken the beginning of a State Forestry Survey along ecological lines. The object of the Survey is, first, to determine the extent and composition of the forests of the State, second, to determine the areas that should be kept in permanent forests either as natural history preserves or for economic utilization, third, to determine the areas that should be afforested or reforested and the tree species that should be utilized therein, and fourth, to determine in the several counties the areas best suited for natural history preserves in connection with the State Forest Reserve Act now in force. From time to time it is expected to publish partial reports with maps and descriptive texts of the counties or parts of counties studied. The speaker has assumed responsibility for and begun work in Cook County and several of the adjoining counties in the north-eastern part of the State, and several other ecological workers have already assumed responsibility and begun work in some other counties.

Shreve, Edith B., Desert Laboratory. "The Role of Leaf Temperature in the Determination of the Index of Transpiring Power of Leaves."

The use of tripartite cobalt paper slips for determining the foliar transpiring power of leaves depends on the assumption that the slips are at air temperature. Determinations of the temperature of the slips made with the thermo-couple apparatus for leaf temperatures show that this assumption may be made with an error usually 2 per cent. and never more than 8 per cent. Standardization of tripartite slips should be made within 2 or 3 degrees of 20° C. in order to make it safe to use air temperatures in the calculations.

Shreve, Edith B., Desert Laboratory. "A Method for Determining the Surface Temperature of Leaves."

Describes a method by which a thermo-couple and portable galvanometer may be used to secure surface temperature of leaves to within 0.1° C. The apparatus requires no ice nor warmed water and is suited to field and laboratory use.

Whitford, H. N., Yale University. "The Forest Formation of British Columbia."

Need of the subdivision of the western coniferous forest formation has already been recognized. Danger of making too many or too few types. The grouping of distinct formations is often necessary for graphic presentation. Differences due to altitude and latitude should be more recognized in delimiting the formations. Brief description of the primary and secondary formations, and of the most important successive stages.

**STUDIES IN THE ECOLOGY OF TROPICAL
RAIN-FOREST :**
**WITH SPECIAL REFERENCE TO THE FORESTS OF
SOUTH BRAZIL¹**

By R. C. McLEAN.

PART I. HUMIDITY (*concluded*) AND
PART II. ILLUMINATION.

(*With ten Figures in the Text.*)

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¹ The first portion of this paper appeared in this JOURNAL, 7, pp. 5-54, May, 1919.

PART I. HUMIDITY (*concluded*).

SECTION B. SOIL HUMIDITY.

(a) DESCRIPTIVE AND WATER CONTENT OF SOIL.

1. **General Descriptive.** The origin of the soil upon which these forests grow is not at all clear.

The underlying rock is gneiss, tilted in many places to high angles by the intrusion of granite; but the sub-soil has little in common with the gneiss, and does not appear to have been derived from it. The status of the soil, as sedentary or transported, is therefore uncertain. It may quite probably be of sub-aerial deposition. The sub-soil is a hard substance, bright red-ochre in colour, and of very uniform consistency. It is coarse-grained and brittle, and but for the fact that its chief constituent is quartz, it resembles nothing so much as powdered brick. This peculiar deposit is of considerable depth in the valleys, as much as 10–15 feet in some places, but it dwindles to a foot or so before one has mounted far up the hillsides.

There seems to be much in common between this deposit and the "Laterite" of S. India and Ceylon, and I am inclined to regard it as a slightly differentiated form of the same substance, chiefly distinguished by its softer texture. True laterite is almost as hard as rock, but this stuff can be crumbled in the hand.

Laterite is currently regarded by geologists as of sub-aerial origin, and several things point to the same conclusion in this case, namely: the uneven thickness of the deposit, the greatest depths being at the lowest levels; the great uniformity of grain and texture, which suggests material sifted by some agent such as wind; also the frequent inclusion of boulders and pebbles of granite and almost unweathered gneiss. Further than this there are however no data to guide us.

The sub-soil passes with great abruptness into the soil. On large cleared areas, and near the shore, true soil is non-existent and the red laterite forms the surface; but in the forests it is covered by a true soil.

This soil is extremely shallow; 10 centimetres is a general average depth for the hill-forests. The great depths of humus soil spoken of by some of the older travellers occur only in valley forests and even there only exceptionally, where circumstances of topography have favoured accumulation. This shallowness of the soil has not been generally emphasized by those who have written about tropical rain-forests, but its effect on the vegetation is manifest.

The soil is very loose, open and coarse-grained. It is poor in humus as a whole, though the humus content is greater on flat areas, and the valley bottoms, consequent probably on reduced percolation. The humus is at its least on the steep, rapidly drained hill-sides. The soil is light-brown in colour and powdery when dry. It might, in a sample, easily pass for a particularly light and rather sterile soil of our own country, but closer examination reveals great divergences. The basis of the soil is quartz sand with subangular grains, as in the sub-soil, and when the organic matter is removed by ignition the same ochreous colour is revealed. The immediate origin of the soil is, then, the underlying laterite, whatever may have been the ultimate origin of that deposit.

In accordance with its general character, the soil has a very low capacity for absorbing or retaining water; but in this latter respect its power is enhanced by the layer of decaying leaves 2-3 inches thick which everywhere covers it. This layer is not seasonal as with us, but perpetual, owing to the high percentage of evergreen trees present, so that while being continually destroyed by decay it is as steadily renewed. Thus its effect is continuous through both wet and dry seasons, and may even be accentuated in the latter case, owing to the more profuse phylloptosis.

The constant excavation of the soil by mammals and the large Iguana lizards is a noteworthy factor, especially in any consideration of nitrification.

2. Water Content. The water content of such a soil as that above described can never be very high. The holard and the hygroscopic water were estimated for the three following stations in the forest:

Station A was that used for the experiments dealt with in Section A, and therein referred to as the "Base Station." This was at the foot of the hill, only some 50 ft. above sea-level.

Station B was half way up the hill side, on very steep ground, where the bushes of the undergrowth were scanty.

Station C was close to the summit of the hill, at the fringe of a society of *Asterocaryum* palms.

Representative samples were taken from each station, under different weather conditions. After clearing away the layer of decaying leaves, the surface of the soil was scraped off and the samples taken represented soil between 1 and 12 cms. depth. Each sample weighed approximately $\frac{1}{2}$ kilogramme.

These samples were spread out in zinc pans and air-dried in the sun for several days, the resulting loss in weight being regarded as the normal moisture of the soil or "free-water." The air-dry sample was then dried at 100°-110° C. and poured hot into an air-tight tin to cool. The consequent loss of weight is called "hygroscopic water."

The results obtained are tabled below. In each case:

		STATION A	STATION B	STATION C
		gms.	gms.	gms
1st Estimation, after 10 days drought	(1)	8.25	8.4	6.8
	(2)	.55	1.2	1.5
2nd Estimation after 1.7 mm. of rain	(1)	8.03	8.04	11.09
	(2)	1.57	1.76	2.01
3rd Estimation after 13.8 mm. of rain	(1)	9.6	11.2	11.5
	(2)	1.2	1.2	1.8
These figures represent the weight of water in 100 gms. of the wet soil.				
The averages are 	(1)	8.6	9.21	9.79
	(2)	1.1	1.38	1.77

(1) = The "free" water, (2) = The hygroscopic water.

Soil from Station A which had been brought to England and kept dry for three years was again examined for its hygroscopic moisture and yielded 1.128 per cent., which agrees with the average in the fresh soil. The colloid hygroscopic materials had not, therefore, been destroyed, by the long drying. The water content of the sub-soil varies of course with other factors, independent of precipitation, so that full estimations of it are necessarily complex. The hygroscopic water in a sample from the top of the sub-soil shows a rather higher value than the soil from Station A, namely 1.268 per cent. Comparing the stations with one another it is evident that C became the driest of the soils in drought, but picked up much more water than either B or A from the same amount of rainfall. This may perhaps be accounted for by an opposition between higher saturation capacity than A or B, but more effective drainage, owing to its situation on the hill top, although it is more likely that it is associated with the better access of the rain to the soil. The explanation of this curious observation is considered later, in sub-section (c). To determine what influence the hygroscopic water might have upon the drying out of the forest soil, and its relationship to the holard, careful estimations were made of its variation compared with the Relative Humidity. If the hygroscopic capacity were unusually high, might it not under circumstances of drought become a limiting factor in determining vegetation? In the present instance especially, where there is a very porous soil in conjunction with a very humid atmosphere, it might be significant.

(1) The following were the percentage weights of water absorbed by hygroscopicity:

Sample A. 1. Dry weight, 425 gms.

Absorption, .013 gm. of water per 100 gms. of soil (air dry basis)
per 1 per cent. rise of Relative Humidity.

Sample B. 1. Dry weight, 462 gms.

Absorption, .011 gm. per cent., as above.

Sample C. 1. Dry weight, 539 gms.

Absorption, .023 gm. per cent., as above.

Taking the weight of oven-dried soil as basis, the amount of water absorbed per cent. per 1 per cent. rise of Relative Humidity was:

A. 1. .094 gm.

B. 1. .086 gm.

C. 1. .074 gm.

(2) More delicate measurements, made with smaller quantities, over a considerable range of Humidity, are plotted in the graphs in Fig. 1, where the close relationship of the two factors is evident. To see what effect this

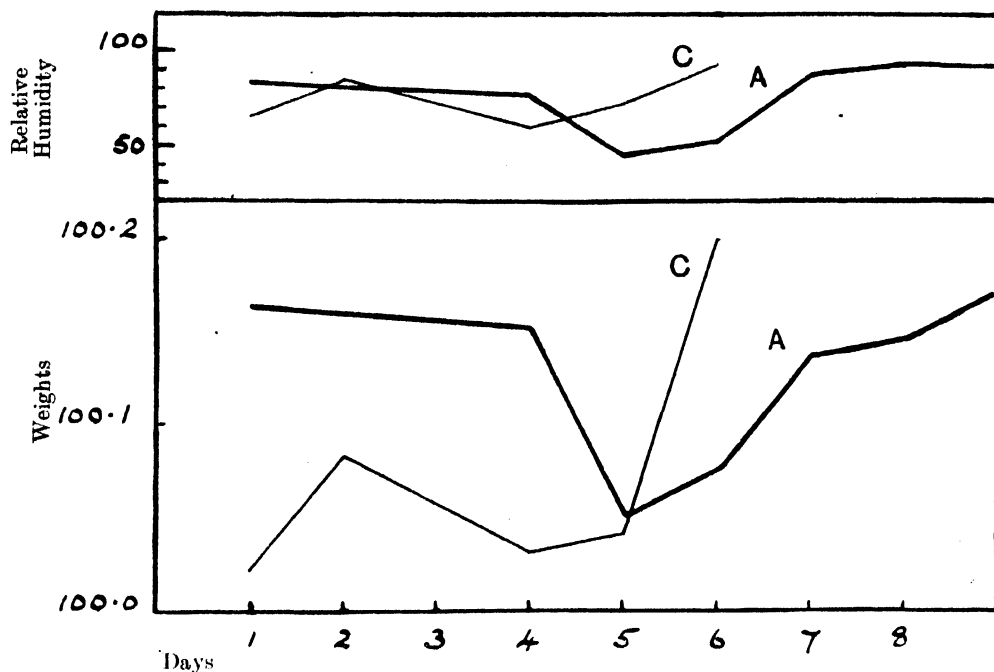


FIG. 1. Hygroscopic Variation in the weight of dry soils compared with the simultaneous variation of Relative Humidity. The thick lines are the weights of soil from station A with the corresponding Humidities. The thin lines are the same measurements for a sample of dry soil from Station C.

hygroscopic power has on the amount of water present in a given mass of soil, the true density of the soil must be known. This in *Sample A* (1) was determined to be 2.12, and in *C* (1) 2.23.

Only soil in contact with the non-saturated outer air would be liable to fluctuation of hygroscopic moisture, so that 1 cm. is sufficient depth to consider from this point of view.

Station A. Spec. gravity of soil 2.12: therefore 1 sq. metre to 1 cm. depth contains 21.2 kilos.

Absorption, .13 gm. per kilo per 1 per cent. rise of Relative Humidity, that is, 2.75 gms. per sq. metre.

Station C. Spec. gravity, 2.23: 1 sq. metre to 1 cm. depth contains 22.3 kilos.

Absorption, .23 gm. per kilo per 1 per cent. rise of Relative Humidity, that is, 5.12 gms. per sq. metre.

On the basis of the oven-dried weight¹, the total water held hygroscopically by 1 sq. metre of soil to 1 cm. depth in *saturated* air would be:

A. 1.99 litres.

C. 1.64 litres.

These figures are very considerable, so large in fact that if normally moist soil takes up hygroscopic water from the atmosphere it must be a powerful element in determining the available water supply, if it is absorbed from the soil colloids by the vegetation.

It is interesting however to note that after 13.8 mm. of rain when the air in and immediately above the soil was saturated, the total water content at Station A. was only 2.3 litres in all, to the same depth as above, and even allowing for percolation (the sample was taken directly the rain ceased) and for diminished access of rain to the soil owing to the canopy of foliage, it is very improbable that only .4 litres should have been contributed by the rain, or that moist soil functions hygroscopically in the manner suggested by examinations of dry soil. This is in agreement with the work of Keen (1914), who finds no discontinuity of state in the water held by a normally moist soil.

3. Mechanical Analyses of the Soil. Mechanical analyses of the raw sub-soil and of soil from Station A were made by the sedimentation method, using air-dry "fine" soil, i.e. powdered with a wooden pestle. The results are given in the table below:

	Above 3 mm.	3 mm.-1 mm.	1 mm.-.2 mm.	Fine Sand	Coarse Silt	Fine Silt	Clay
Raw Soil	0 %	21.2 %	21.6 %	6.95 %	34.2 %	7.07 %	.82 %
Forest Soil	0 %	9.63 %	56 %	12.64 %	6.21 %	5.7 %	.56 %

Mechanical analysis of soil from a bare patch outside the forest compared with soil from Station A, inside the forest, in both cases omitting humus from the estimations.

In the "Raw Soil," that is to say in the sub-soil immediately beneath the soil, the clay fraction is not quite fully represented by the figure given, for after nearly three weeks of daily sedimentation the supernatant liquid was still turbid at the end of 24 hours settling. The turbidity was so slight that the attempt to remove this last and finest fraction was abandoned. The actual weight of material lost must have been almost infinitesimal when the total collected only amounted altogether to .82 per cent., a surprisingly small amount. The sub-soil is a comparatively impervious medium, as the large proportion of finer constituents would indicate, and no doubt the exceedingly fine grained clay must be largely accountable for this. It also gives the sub-soil considerable absorptive power, besides playing a colloidal part in retaining

¹ See top of previous page.

water. In itself the clay fraction seems too small to accomplish this, but the high percentage of smaller medium-sized grains, the "coarse silt," would afford an opportunity for close interpacking of the grains which would very greatly reduce the internal space.

The coarse-grained character of the "Forest Soil" is evident, and the aggregation of the elementary particles by humic cement has tended still further to increase the porosity. At the same time it is probable that much of the finer material may have been bodily washed downward through the soil by the rain, whose great mechanical force must always be borne in mind in dealing with a tropical soil. The result, however arrived at, is that the surface soil is greatly opener and more porous than its substratum.

(b) RELATIONSHIPS TO RAINFALL.

1. **Saturation Capacity of the Soil.** The total water absorbing power of the soil was estimated in various samples. The results are tabulated below:

Water Absorbing Capacity.

Station A. Sample 1 as taken for estimation of the water content. Two fractions used.

Averages. Weight of dry soil, 87.98 gms.

Weight of water absorbed, 37.45 gms.

Weight of water absorbed per cent. of the dry soil, 42.56 per cent.

Station C. Sample 1 (hill-top). Two fractions as before.

Averages. Weight of dry soil, 157.94 gms.

Weight of water absorbed, 62.15 gms.

Weight of water absorbed per cent. of the dry soil, 39.5 per cent.

Sub-soil. One estimation.

Weight of water absorbed per cent. of dry soil, 44.0 per cent.

Referring back to the figures previously given for average water contents, we see that under ordinary conditions of moisture, e.g. after a short fall of rain succeeding a drought, the forest soil only contains 20–25 per cent. of its saturation capacity. Considering the open character of the soil this is perhaps fairly high, but Hellriegel, quoted by Hall (1912) gives 40–50 per cent. of saturation as the best water content for most soils, that is to say a content which removes the possibility of water supply being a limiting factor. This case is far below that level, so the possibility of the ground water being here a limiting factor, at least under some circumstances, cannot be ruled out. It is curious to note that although the water absorbing power of the soil at Station C is *lower* than that at Station A, yet a similar amount of rainfall (see the 2nd and 3rd estimations of holard on page 124) produced a *higher* water content. This fact we noted previously, and it is now seen to be inconsistent with the absorption capacities. Two explanations present themselves; either

the water retaining capacity of the soil at Station C is higher, or the rainfall has unequally affected the two localities. They are too close for us to believe that the actual precipitation was different, but something may have diminished the value of the rainfall to the soil of Station A below that at Station C. The first hypothesis leads to a consideration of the retention capacities of the two soils under similar conditions. The soil was enclosed in a cylinder made of stout grey filter paper, bound together with surgeon's plaster at top and bottom. The air-dry soil is filled into this (about $\frac{1}{2}$ kilo was used) and tapped gently to settle down. This cylinder is placed in a shallow saucer of distilled

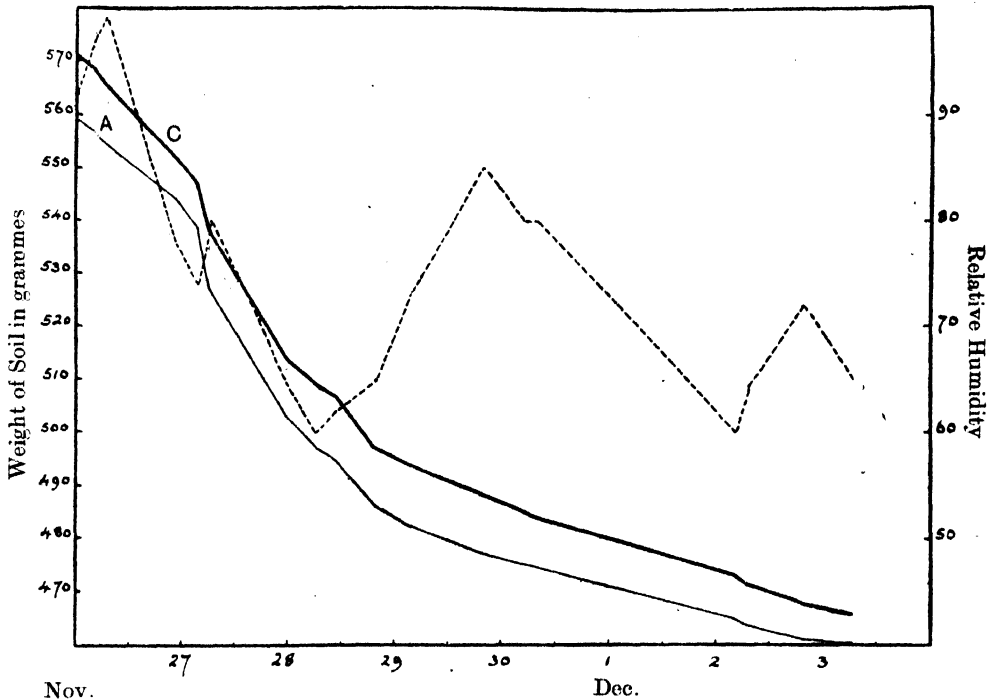


FIG. 2. Graphs illustrating the rate of drying of two soil samples from stations A and C respectively. (A, thin line; C, thick line.) The variation of the Relative Humidity is shown by the broken line. Drying takes place in a continuous logarithmic curve, showing very little relation to the humidity curve. There is no evidence of any hygroscopic variation of water content in the moist soil.

water and left until the soil is completely saturated, lifted out, and, as soon as dripping ceases, superfluous moisture is wiped off the outside and the whole placed in the middle of a large filter paper in a saucer, the filter paper ensuring that percolating water does not collect beneath the cylinder. The accessories are weighed together beforehand, so that the actual weight of soil may be known, the paper cylinder being first carefully wetted to avoid the error otherwise arising from its own imbibed water. By periodical weighings of such an apparatus, the progress of the process of drying may be followed, and correlated with the humidity of the surrounding air. The curves resulting

are shown in Fig. 2, alongside of the Relative Humidity. The curves are of a simple logarithmic type, tending towards horizontality at the "air-dry" point, where it is in equilibrium with the atmospheric moisture and beyond which it fluctuates with the Relative Humidity. The direction of the curve is of course sensibly affected by atmospheric moisture, but it is important to notice that the downward course is nowhere interrupted. As we have seen from the measurements with "dry" soils the contained mass of hygroscopic water should theoretically bear a large proportion to the total water content in moist soils, but in the evaporation curve from these moist soils there is no trace of the accretion of moisture by hygroscopic action following a rise in atmospheric humidity. The drying process continues steadily. This may be a crude representation of the facts, but it tends decidedly to emphasise the view we have previously expressed that moist soil does not contain "hygroscopic" water, but that all the water content is in the same physical state. In this connection the refined experimentation of Keen (1914) is interesting. His examination of evaporation from soils as contrasted with pure sand led him to the conclusion that there is no "hygroscopically" held moisture in wet soils, but that all water present is held by the soil particles, not as superficial films, but colloiddally imbibed by the clay fraction of the soil, which is regarded as partly if not mainly responsible for the curve of evaporation from the soil.

This is quite in accordance with the view expressed here. When the soil is dried out, however, surface hygroscopicity seems in some way to replace the more intimate relation of the colloid particles and the water in moist soil. The apparatus here used serves to show both the loss by direct evaporation and by downward percolation, so that it gives a measure of total retentive power for the soil.

For our immediate purpose the curves serve to show that the total retentivity at Station C is not in excess of that at Station A, which invalidates the first suggestion to explain its higher water content.

The second alternative hypothesis, i.e. that concerning the access of rainfall to the soil, will be considered separately under the next subsection.

Under the present heading should be included however some further comparison of the porosity of the forest soil with its sub-soil. The relatively high saturation capacity of the rather open forest soil is surprising. In this soil 50 per cent. of the soil is in particles between 1 mm. and .2 mm., which implies a very coarse texture, and yet this soil absorbs about 40 per cent. of its weight of water. It is possible perhaps that this may be due to the packing of the grains reducing the pore space, as in the parallel case of the red sub-soil, or to the content of organic colloids.

Percolation is however very rapid through the moist soil. This was measured with columns of water-saturated soil in glass tubes 2.5 cms. in

diameter: red soil 58 cms. long, brown soil 55 cms. Time taken between commencement of water dropping on to the upper end of the soil column, and commencement of dripping from lower end:

Red, 15 mins.

Brown, nil.

This is not of course equivalent to the rate of percolation through the soil at stages short of complete saturation, but this rate must be infinitely variable, so that the saturation point is the only constant by means of which soils can be compared. The columns of soil were allowed to drain for 115 days in order to bring the water content down to its percolation-free minimum. By this time the soil at the open ends was air-dry, percolation had ceased and therefore water was being lost only by evaporation. The brown soil only was examined. In this condition soil just below the actually dry layer contained 5.6 gms. of water per cent. of the wet soil; (compare normal water contents given in table, page 124). The growth of *Chlorella* and a fern prothallus more than a foot below the surface of the soil in the draining column may be taken as further proof of the great porosity of the soil. The sub-soil being relatively impervious, drainage must run chiefly through the soil layer itself, but, owing to the high angles of the ground, it is quick; the soil being rendered still more pervious by rootlets, decay and the cementing action of the humus in agglutinating the clay particles. This may serve to indicate why humus tends to accumulate in valley forests; the soil there being less drained and so much richer in water.

On such a shallow and porous soil anything in the nature of upward soil osmosis, or Lynde's effect, is out of the question. The clay content is too small to form a "membrane." Moreover the constant precipitation not only quite prevents any concentration of mineral salts in the upper layers but tends to reduce the concentration already existing so that salts are much more likely to be lost into the sub-soil than the reverse.

2. **The Idea of "Rainfall Efficiency."** To shelter under a tree when the rain comes on is one of the most natural and most obvious actions, and like many of our instinctive doings it seldom attracts the examination of our reason, or it would become plain that the tree which gives temporary shelter to the botanist must be a permanent shelter to itself. The ecological importance of the light stopped by the crown of a tree has long been recognised and has been clearly formulated by Wiesner, but the parallel effect on rainfall seems to have escaped expression. The case of the isolated tree is not, however, a perfect illustration of our principle, for not only do its roots often spread beyond the shelter of its canopy, but also percolation from the open ground close by and the general drainage of the ground, supply the surplus water, no matter how little finds its way directly through the crown of foliage. The effect is not to be seen properly in such examples, but rather in true associations of the natural vegetation. Nor is the effect confined to trees alone. In every type of plant association, closed or open, woodland, bushland or prairie, some

checking of the rain by the aerial parts of the plants must occur, lessening the actual supply to the soil. This water, thus held back, is only in the rarest cases directly beneficial to the plants concerned, and even in the exceptions the benefits conferred are usually subsidiary to the paramount necessity of root absorption. Such rain, therefore, caught by leaves and branches and directly re-evaporated, is to all intents and purposes lost to the plants, directly reducing the efficiency of the total rainfall as far as that association is concerned, without taking into consideration the possible effect upon stomatal transpiration, which may bring about a further indirect reduction of efficiency. It will readily be imagined that this reduction in rainfall efficiency may under some circumstances be of limiting importance to the vegetation and the strict consideration of this neglected factor may prove fruitful as a key to the understanding of plant form. Incidentally, we may perhaps see in it the reason why leaf mosaics are not more perfect than they are; or, in another direction, the force which prevents some associations on dry soils from becoming closed.

The idea of rainfall efficiency is that of the percentage of the total rainfall descending on a given area which becomes effective in the soil, allowing not only for the stoppage of the water mechanically by the leaves, but also for the effect of drainage in the soil itself.

Practically, it means the ratio between the actual water content of the soil immediately after rain, and the total water content which the given amount of rain should produce, apart from the two factors of decrease mentioned above. The closer the association, the smaller will be the effective percentage, while *ceteris paribus*, a bushland will have to submit to a lower efficiency than a grassland and a forest association than a bushland. In associations where a seasonal change of physiognomy occurs, e.g. in deciduous silvae, there will be a corresponding fluctuation of the efficiency. The efficiency thus considered is a function of both density and drainage; it need not include a consideration of the varying biological capacities of the plants themselves in making use of the water obtained, as this is obviously subsidiary and subsequent to the action of the two simple factors controlling the obtainable water.

The practical method adopted for working out the efficiency in the case of this forest was as follows. The necessary data are: the water content of the soil just before and after a known depth of rainfall, the depth of the soil and its specific gravity. If the rainfall is very heavy or the soil very shallow or sandy, the saturation capacity of the soil should also be ascertained as a check.

My calculations were made on the basis of an average water content, so that they are only approximate. The holard should be taken directly before rain, but this was not foreseen when I was on the spot. Still, as the average was based on readings taken under conditions varying from drought to heavy rain, it should represent pretty closely the amount of water in the soil after

two or three dry days, which was the condition at the beginning of the fall of rain which was employed for this measurement.

The specific gravities were found by displacement, the medium employed being benzine of specific gravity .660.

Station A. Foot of hill. Mixed sample. Spec. gravity, 2.12.

Station C. Top of hill, near palm society. Spec. gravity, 2.23.

Hall (1912) gives 2.65 as the average specific gravity of cultivated soils. The lightness of these is probably due to the admixture of fine ferric oxide with the sandy basis.

Rainfall Efficiency.

Station A.

Average holard per 100 gms. of soil, 9.7 gms. (Taken as representing holard before rain.)

Rainfall, 13.8 mm.

Holard after the rain, 10.8 gms. per cent.

13.8 mm. of rain on 1 sq. cm. surface, 1.38 gms. of water.

Depth of soil, 10 cms.

Volume of soil receiving above amount of rain, 10 c.c.

10 c.c. of soil weighs 21.2 gms.

Average holard of 12.2 gms. 2.05 gms.

Rise in water content following the rain, .23 gms.

But theoretical amount of water supplied, 1.38 gms.

Therefore at end of rain only 16.6 per cent. of this theoretical total was to be found in the soil.

Station C.

Average holard, 11.6 per cent.

Rainfall, 13.8 mm., representing 1.38 gms. of water per sq. cm.

Weight of soil receiving this water $10 \times 2.23 = 22.3$ gms.

22.3 gms. contains average holard of 2.57.

Rise after rainfall, .38 gm. (which is 27.5 per cent. of the theoretical).

As this gives us a measure of the direct effect of the floristic composition of a plant association on its water supply, it seems desirable to facilitate the work by casting it into the form of a single mathematical expression. The rainfall efficiency equals:

Rise in water content of mass of soil with 1 sq. cm. surface area $\times 100$, divided by weight of rain falling on 1 sq. cm.

Let D = depth of soil in cm., G = specific gravity. Weight of rain falling on 1 sq. cm. = height of rainfall expressed in cm. = R .

H_1 = water content of soil before rain per 100 gms. of soil

H_2 = " " after " " "

$$\text{Then } \frac{\frac{DGH_2 - DGH_1}{100} \times 100}{R} = \frac{DG(H_2 - H_1)}{R}$$

Referring back to the graph of the drying rate of the soil it will be seen that in the first few hours the loss of weight was small, only about .4 per cent. of the soil's weight during the first three hours, so that in this calculation of rainfall efficiency but little can be reckoned as having been lost to the soil by drying, as the samples were taken immediately the rain ceased. The only other probable supposition is that it had not reached the soil. Station C is thus found to have a higher rainfall efficiency than Station A, which I believe to be the explanation of the higher water content found after a slight rainfall, although the soil had previously been drier. These facts are I think worth this consideration, for they have a much wider bearing ecologically than the elucidation of a single peculiarity.

3. Discussion of the Rainfall Efficiency. There can be little doubt that the idea here expressed is one of widespread significance to vegetation, a factor which may become in some conditions the determinant of the prevailing facies. It is a very simple and obvious idea at most, but though often implied in ecological writings, has not hitherto been formulated. Even this mere formulation of an idea, which is all that has been attempted here, has such a decided value that it is a pity it is avoided by so many workers in cases where strict proof is not immediately available. Formulation clothes an idea with an objective reality, reducing it to a plane upon which it can be subjected to logical and experimental tests, both alike impossible until an idea has passed beyond implication to the stage of categorical expression. The fundamental importance of expression, as opposed to implication, is one of the bases upon which descriptive science must rest its claim of philosophical validity.

The rainfall efficiency would appear to be one of the most powerful influences in eliminating forest associations under diminishing rainfall, as such associations themselves effect a further diminution of rainfall up to 80 per cent. of the total received. There is a probable correlation between the high efficiency of grass-land and its existence in areas of scanty rainfall, where but for this efficiency its superficial hold of the soil would inhibit its occurrence. It would be interesting to see whether different types of woodland could be correlated with differing rainfall efficiencies. Theoretically the woodland of low efficiency should be confined to areas of high rainfall or very retentive soil, though of course it must be recognised that the general drainage of an area may affect the efficiency in either direction.

(c) CONSTITUTION OF THE SOIL.

1. **Analysis of the Soil for Crystalloids.** Analysis of several constituents has been carried out with samples of soil from Station A.

Perhaps the most significant of the mineral salts is calcium carbonate.

Fine air-dry soil was analysed in a Schrodter flask. There was a scarcely perceptible loss in weight, indicating a carbonate content of about .09 per cent., a very low figure indeed, soils with as little as .1 per cent. being decidedly uncommon. The effect of this is definitely to place a restraint upon the nitrification of the soil, and upon the liberation of nitrogenous reserves in humic decomposition. The amount of "available" phosphoric acid present in the forest soil, estimated by the arbitrary system of extraction with a 1 per cent. citric acid solution for seven days, proved to be also very small indeed, being .0087 gm. per cent. of the weight of dry soil taken, and the amount of potash extracted by the same method was infinitesimal, too small for estimation within the limits of useful probability. Although such measurements are conventional they serve a useful purpose in this case at least in emphasising clearly the poverty of the soil in manurial elements and they are significant in view of the imperfect progress made in reclaiming such land agriculturally. To speculate as to the probable causes of this shortage of essential minerals is perhaps unprofitable, but one may surmise that primarily the origin of the soil may be to blame, and that secondarily the very heavy rains and the rapid percolation have together contributed to leach the soil. The inorganic crystalloid which bulks most largely in analysis, though not the most significant from the plant's view-point, is ferric oxide. The raw sub-soil in fact consists of little beside ferric oxide and quartz. Iron estimation is easily effected by solution in strong hydrochloric acid and subsequent reduction. In the case of the raw sub-soil it totalled 20.0 per cent. by weight of the dry soil, and in the forest soil 5.25 per cent. of the air-dry soil or 5.8 per cent. of the ignited soil. From this latter the humus has disappeared, the underlying red coloration being made clearly visible. These estimations are best performed with small portions of soil, 5 gms., not more, powdered very finely in an agate mortar, as otherwise the bulk of precipitated ferric hydroxide is too great to be easily handled.

The total matter extractable by hydrochloric acid, apart from the iron oxide, is strikingly large in comparison with the minute effect of citric acid. Forest soil was digested in conc. HCl for three days at 60° C. and the loss in weight of mineral matter thus dissolved was 32.3 per cent. of the original dry soil¹. Subtracting from this 5.25 per cent. of Fe_2O_3 we get 27.05 per cent. of soluble mineral matter. Time unfortunately prevented the completion of this analysis, but the total amounts of phosphoric acid and potash present in the soil must be, on this showing, very considerably greater than is indicated

¹ The *humus* does not appear to be attacked by hydrochloric acid.

by the citric acid estimation, which gave such a small result of available salt as to suggest considerable doubt as to its validity.

2. Analysis for Colloids and Nitrogen. There is some difficulty in estimating the organic content of the soil owing to the amount of reducible ferric oxide present. This affects the sub-soil more particularly, but no doubt increases the apparent humus content of the top soil as well, for the removal of the humus by ignition reveals the presence of quantities of iron oxide, as in the sub-soil. Ignition at a low red heat produces the following loss in weight:

Brown top soil, 5.9 per cent.

Red sub-soil, 8.89 per cent.

The latter is certainly an impossible figure, for the soil shows no trace of humus coloration in the fresh state. The proportion of ferric oxide in the two soils is as 5.25: 20. Allowing for this reason a proportionate deduction from the first of the above figures, we find that the top soil contains approximately 3.59 per cent. of humus. This is by no means high, in fact it falls below what is found in ordinary agricultural soils in temperate regions, and does not tally with a conception of great richness in the soil of the jungle. The coarse mechanical structure of the soil, implying a small total surface, enables even this small amount of humus to colour the soil considerably more than one might expect, an accident which may have fostered the older opinions on the subject.

The safer method of estimation, indicating the relative solubility of the humus, and hence presumably its availability to the plant, much in the way that the citric acid extract deals with the mineral reserves of the soil, is by solution in 4 per cent. ammonia. The soil is continuously agitated in ammonia for 24 hours, allowed to settle for two or three days and the amount of organic matter in the supernatant solution found by evaporation of an aliquot portion and gentle drying. Treated in this way the soil yielded 2.53 per cent. of humus in the air dry soil, and judging by the resulting decolourization this must represent very nearly the whole of the humus present. If the estimate of the total humus in the last paragraph is correct, then only 1.06 per cent. is insoluble in ammonia; none apparently having been removed by the preliminary treatment with hydrochloric acid.

The most significant fact with regard to the humus is probably its nitrogen content. The nitrogen fraction is high in this case, being .225 per cent. of the dry soil, or 8.9 per cent. of the soluble humus. Where the humus content of the soil is low its proportional content of nitrogen is almost always high, according to Hall. This seems to be due to the greater potency of fermentative over nitrifying reactions in certain soils. In this case the high temperatures, heavy rainfall and good aeration cause a very rapid breakdown in the carbonaceous materials of the humus, with a rapid reduction of weight and the evolution of a great deal of CO_2 ; but nitrification is impeded by the absence of a suitable base to form nitrogen salts. The proportion of nitrogen in the

soil throws very little light on the actual amount available for the plants, and it is a matter of observation that soils containing much soluble humus yield nitrogen slowly to a crop, apparently because the process of rendering available the nitrogen reserves of the humus goes on but slowly. It is impracticable to estimate from the soil the amount of available nitrogen. This can best be gauged from crops. The amount of humigenous material entering the soil must be very great indeed in the case of a rain forest, but the destruction by fermentation is so rapid and thorough that only a small quantity of actual humus, rich in nitrogenous substances, is formed. This may be still further reduced by the rapid percolation of a heavy rainfall, so that the nitrogen reserves are not as large as would be anticipated. The absence of an available mineral base renders it unlikely that a large proportion of the humus nitrogen is actually made available for the vegetation.

Of actual nitrogen fixation there is probably little, if any, for soil is decidedly acid. The other conditions, temperature, aeration and water content, are altogether favourable, the absence of the base alone prevents the soil becoming very rich in nitrogen. On the point of water content, Lipman and Sharp (1916) have shown a content of 20–24 per cent. of saturation in the soil (air-dry basis) to be the most favourable to nitrogen fixation, a condition corresponding closely to that normally found in these soils.

The condition in the forest seems to be that of a soil rich in humigenous material, yielding nitrogen but slowly to form assimilable compounds, and almost an impossible medium for nitrogen-fixing micro-organisms. The effect of clearing is tremendous. Burning must result in complete sterilization, where such heavy vegetation is consumed on a shallow soil, but apart from this the supply of humus is cut off, increased aeration assists in the break up of the remaining humus with the disintegration of the compound particles of the soil. Periods of sun-drying followed by very heavy rainfall on the now undefended surface provide ideal conditions for almost complete removal of the humus or its soluble derivatives. Given the initial poverty in mineral salts, the result is a substratum which is of no value to anything but the roughest and hardiest of plants.

An attempt has been made to compare the soluble crystalloids with the soluble colloids. Water-soluble crystalloids extracted from the dried soil amounted to only .18 gm. per cent., although the HCl extract showed over 30 per cent. of crystalloids to be present. The amount of soluble humus is 2.53 per cent., as shown above. It seems fair therefore to regard the soil as a colloid soil, that is to say "geloid" according to the classification of Gola (1910).

3. The Soil Solution and Mycorrhiza. The possibility that an estimate might be made of the hydrogels in the soil, or rather of their importance in the adsorption of salts, led to an examination of the soil solutions by a process of differential extraction, in the manner described below. The basis of the

method was the hypothesis that by drying out, the precipitated hydro-colloids would be forced to liberate their adsorbed compounds. If then the soil be rapidly flushed with water, part of which can be at once removed, and the same soil be then allowed to stand in a saturated condition for some days, until the hydration of the gels allows them to reabsorb salts which had been at first taken up by the water, then the difference in concentration of the first extract and the second, obtained after standing, might afford at least a comparative measure of the adsorptive powers of the soil in question. In order to test this, both soil and sub-soil dried in air and rubbed down with a wooden pestle were filled into glass tubes covered at their lower ends with soft linen, in columns $24'' \times 1''$. The lower ends dipped into distilled water, which was drawn rapidly up by an air pump, until water rose about one centimetre above the upper surface of the soil column. Air was at once readmitted and the surplus back-flow collected from the lower ends as the "1st Extract." The soils, now fully saturated, were allowed to stand from Oct. 30th.-Nov. 11th, i.e. 13 days, the lower ends dipping into beakers containing a known quantity of distilled water in order to maintain saturation. This was I think needless, but it was not allowed to affect the result. Corking the tubes at the top would have sufficed to maintain saturation. Each soil column absorbed almost exactly 160 c.c. of water. A corresponding amount was placed in a dropping funnel above each column; next the soil tubes were raised from the water beakers and allowed to stop dripping, then the water from the funnels was allowed to drop very gently on to the upper surface, from a height of 1 cm. at a rate of 10-15 secs. per drop. This water displaces downwards the water which has been standing in the soil, and this is collected as the "2nd Extract." Not more than 100 c.c. was collected in either case, in order to avoid collecting any solution vitiated by admixture with the displacing water, and considering the previous saturation of the soils and the slow rate of downward percolation, there was little danger of this.

These extracts were measured in volume, evaporated down and gently ignited to remove organic substances dissolved out from the humus. The percentage concentrations are given below:

Forest Soil.	(A)	1st Extract	.114 per cent. = 1.9 times <i>B</i> .
	(B)	2nd Extract	.06 per cent.
Sub-soil.	(C)	1st Extract	.01 per cent. = .83 times <i>D</i> .
	(D)	2nd Extract	.012 per cent.

The water in which the bases of the tubes had been standing was retained as "Diffusion Extract." The loss of salt into this solution represents a weakening of the solution in contact with the soil, in addition to that caused by adsorption, so that allowance must be made for this

Diffusion Extract. Soil.	(E)	.032 per cent.
Sub-soil.	(F)	.002 per cent.

Adding these to the strengths of the Second Extracts we find that the proportion between 1st and 2nd Extracts now becomes:

Soil. 1.25 : 1.

Sub-soil. .73 : 1.

But some part of the diffused salts, had they remained in contact with the soil, would probably have been adsorbed, so that the true proportions should be somewhat higher than the above. In other words, the first solution obtained on wetting a dry humus-containing soil is something like $1\frac{1}{2}$ times as strong as the final solution, while in a non-humiferous soil this is reversed, simple solution apparently increasing the strength of the extract when the exposure time is prolonged. This must have a powerful effect on the leaching of soils exposed by clearing, as the alternation of sun baking and torrential downpours of rain provides the best combination for ensuring the most rapid removal of all the adsorbed salts.

That the soil extract contains organic matter is indicated sufficiently by its brownish colour, also a significant index of the presence of unsaturated humus. This is confirmed by the apparent strong acidity of the soil extract to litmus paper. Unsaturated humus has such a drastic influence on vegetation that the osmotic pressure of the soil extracts was determined (by Barger's method) to trace its influence, for admittedly the percentage strength of mineral salts alone is no accurate guide to the osmotic pressure of the soil solution.

The solutions were balanced against sodium chloride and the 2nd Extract was used. This represented the solution in a perfectly saturated soil, a condition almost unattainable under natural conditions in a porous soil like this, so that its concentration may be looked upon as the minimum.

Soil—2nd Extract = .1 gm. mol. NaCl = 4.35 atmos.

Subsoil—2nd Extract = .05 gm. mol. NaCl = 2.17 atmos.

It will be seen that the pressures of these extracts are in no way proportional to the percentage crystalloid strengths, which were in the ratio of 5 : 1; at the same time a minimum osmotic pressure of over 4 atmospheres is remarkably high for a soil which yields so dilute a soil solution, and we can only conclude that the humus is responsible. That "raw" or unsaturated humus is present the reaction to litmus paper leaves no doubt, and it is to this that I believe can be traced in large measure the difficulties in the way of root absorption, remarked upon in Section A as adumbrated by the character of the sub-aerial organs¹. Referring to the work of Gola (1910) as set forth by Cavers (1914) in which an attempt is made to institute classes of habitat based on the soil solutions, the forest in Southern Brazil would fall into that cumbrously denominated "eustatic geloid pedomesophytic." It has been previously remarked that in spite of the open and porous nature of the soil,

¹ See page 42.

the close texture of the sub-soil and the extremely fine colloidal clay which it contains, in conjunction with the great humidity of the air above the soil, maintain a considerable edaphic water supply, so that xeromorphy of the aerial portions is not brought about by direct water starvation. These are not conditions under which unsaturated or acid humus would be expected to form, but there are several peculiarities of the situation which may bear on this difficulty. Firstly, there is the deep shade, in regard to which figures are given under the proper heading in Part II. Secondly, the high soil temperatures. Records were kept of the soil temperatures at the surface and at a depth of 1 foot. These are presented in Fig. 3, where the thick line represents the temperature at the surface, the dotted line at a depth of 1 foot. They are consistently high, but the 1 foot level lags much behind the surface in the higher readings. Lastly there is the very thin layer of almost pure humus lying on

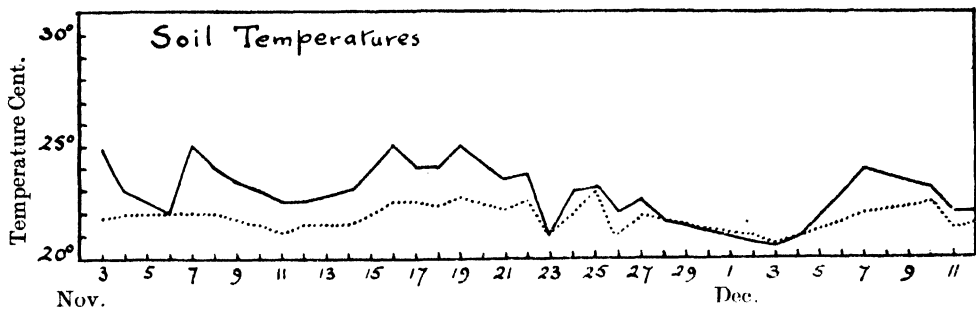


FIG. 3. Soil Temperatures in the Forest, during part of Nov. and Dec. 1912. The continuous line represents the surface temperature and the dotted line that at one foot depth. There is a certain general correspondence in the two curves, which are both on a somewhat high plane, but the surface is liable to greater and more sudden fluctuations. At this time of the year (summer) it is warmer at the surface than at 1 ft. depth, even though under the forest shade.

the soil surface, formed from the perpetual leaf covering, the products from which wash down into the soil itself. This is most probably the source of the unsaturated humus, the effects of which we can trace in the soil solution. Humification goes on chiefly in this compact, water-holding layer, and only to a lesser extent under the better aerated conditions below, in the soil itself; thus paralleling in some degree the conditions obtaining in our own beech woods, but that the rapidity of fermentative decay prevents a like accumulation of humus, at least in most places.

Under such conditions one would expect mycorrhiza to be abundant. This is the case. The humifying layer is very thin, only an inch or so, but both that and the surface of the soil are extremely prolific in mycelia, while the number of mycotrophic plants is unquestionably large.

Janse (1897) gives a list of the mycorrhiza found by him in the forests round Buitenzorg. He examined 75 species, of which 65 came from virgin forest, and 69 possessed mycorrhiza. These figures speak for themselves.

Many of the genera given in his list occur also in the Brazilian forests, and from these data and my own observations the following list of genera known to consist wholly or largely of mycotrophic plants is compiled, exclusive of holosaprophytes:

<i>Lycopodium</i>	<i>Anthurium</i>	<i>Casearia</i>
<i>Selaginella</i>	<i>Paspalum</i>	<i>Eugenia</i>
<i>Psilotum</i>	<i>Ficus</i>	<i>Ardisia</i>
<i>Cyathea</i>	<i>Celtis</i>	<i>Symplocos</i>
<i>Botrychium</i>	<i>Impatiens</i>	<i>Solanum</i>
<i>Araucaria</i>	<i>Vitis</i>	<i>Datura</i>
<i>Curculigo</i> (occurs as a denizen)	<i>Begonia</i>	<i>Rauwolfia</i>
<i>Calamus</i>	<i>Tibouchina</i>	<i>Vernonia</i>

This list is very short, taking into consideration the huge number of species that go to make up a jungle, but it is a very representative one, and judging by analogy with similar woodlands on humus soils in temperate regions, there is the greatest likelihood that many more undergrowth plants will be found to be in the same condition.

Stahl's remarks (1900), that mycotrophic plants are characterized by slow growth and the absence of foliar starch, certainly do not apply to the observed cases in Brazil.

PART II. ILLUMINATION.

(a) NATURE OF THE ILLUMINATION.

1. **General Descriptive.** The great depth of humid air prevailing over the coastal lands of Brazil reduces the heat greatly, but does not affect the amount of light, or only slightly if at all.

From November to March the midday sun is vertical, and illumination at its maximum; but my own hill faced E.S.E., only receiving perpendicular insolation in morning and forenoon. Some idea of the intensity of insolation may be gained from the records of radiation, taken with the black-bulb thermometer *in vacuo* at the Observatory, Rio. These are reproduced in Fig. 4: the readings represent the noontide intensity, and reach a very high level. Solar radiation has for its reciprocal the extent of *nebulosity*. The nebulosity is at its minimum at midday, so that the records of sun radiation given in the graph probably represent the absolute maxima. Annual nebulosity-variation curves show that the period covered by this record is one of super-normal nebulosity. The latter is maximal in the first week of October, minimal at the middle of July. This means that in the cold season clarity of the heavens may compensate for a lesser angle of sun, maintaining thus a high illumination factor, although the heat received has diminished.

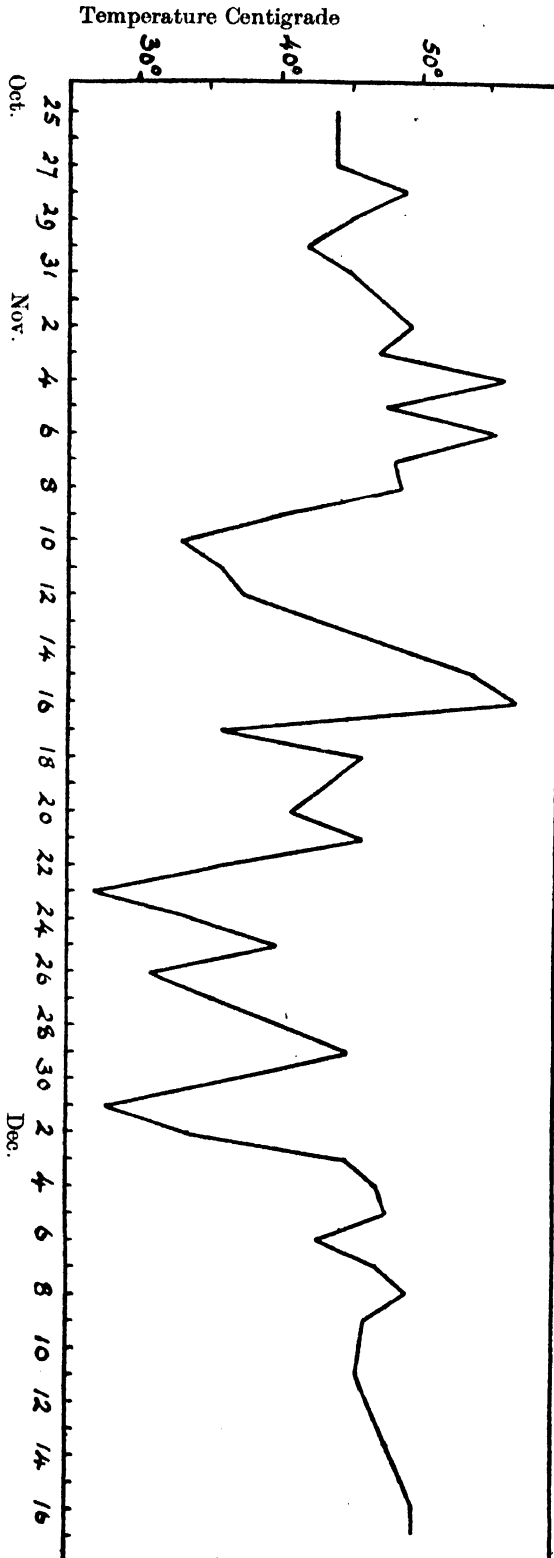


Fig. 4. Solar Radiation Temperatures at Rio Observatory, during the period of work. These measures are from the published records, and serve to show the extremely high insolation that may occur, though on the moister side of Corcovado, where the gardens lie, the range is probably somewhat less.

The upper layers of the forest receive an intense illumination. These layers are the so-called "high forest," the trees of which average about ten feet apart, the spaces between their trunks filled in by a dense mass of shrubs of irregular height and outline forming the undergrowth, beneath which grow in scattered array the lowly herbs of the shade.

The shade cast by the high trees is not at any time very dense in these hill forests, though things may be different in this respect in the valley forests of the Amazon basin, of which wonderful tales are told. The commonest trees are *Mimoseae* with multipinnate leaves, which are nyctitropic. These cast a very thin shade and as the leaflets only "wake" and unfold when full sun strikes them, there is a considerable period each morning when they cast little shade at all. Lianes are important as welders of the tree tops, increasing the shade very greatly. Any increase in shade thrown by the trees acts much more on the shrub layer than upon the ground plants, tending to reduce the three levels of the forest to two. The herbs already endure profound shadow, and thickening of the tree canopy makes small difference to them.

The leaf mosaic of the shrub layer is unusually good, and this divides the forest pretty clearly into two regions, albeit not very evenly or regularly. Above the shrubs the smaller trees and the epiphytes live in comparative light, while below is darkness.

The only other description of the interior lighting of the forest that I know of is that of Lindman (1906). On page 243 of his description of Rio Grande, he speaks of the light as "azul." This is not very noticeable, in my experience, but it is impossible to distinguish by eye the quality of the light apart from the colour of the principal reflecting surfaces, which being mostly leaves give the appearance of a preponderating tinge of green to visual perception.

2. Photometric Measures. Photometric measures were made in simple fashion by the use of an Imperial Photographic Exposure-meter, in which a standard sensitive paper darkens to a standard tint. These exposure meters are very convenient measures for practical purposes, though the results are purely of comparative value and tell one little about the absolute value of the light. Readings were taken both in full sunlight in the gardens and in the forest on the ground level. In order to get a measure of the portions of white light more directly concerned in photosynthesis, that is to say a better estimate of the light as it affects the plant rather than the photosensitive paper, a special gelatine filter was used which cuts off the blue end of the spectrum completely, without appreciably diminishing the intensity of the rest. This very useful contrivance enables one to compare the intensity of the yellow and yellow-green, i.e. the synthetically active rays, under different circumstances. The gelatine filter is supplied by Messrs Wratten and Wainwright of Croydon¹ under the name of "Minus-Blue." It is simply placed over the paper of the photometer and the time of darkening observed as usual. The darkening can

¹ Now a branch of Kodak Ltd.

be observed perfectly through the gelatine. This idea might perhaps be extended to the use of filters passing yellow and orange only, but to make the exposure time practicably short this would mean using a specially sensitised paper, which would prevent direct comparison with the full "white" intensity.

Below are given the readings taken in open sunlight:

Date	White	Minus-Blue
Oct. 26th	3 secs.	30 secs.
„ 29th	2½ „	30 „
„ 30th	6 „	3 min. 45 secs.
„ 31st	2½ „	30 secs.
Nov. 1st	2½ „	30 „
„ 3rd	2 „	27 „
„ 4th	2 „	25 „
„ 5th	2 „	25 „
„ 6th	3 „	30 „

Average ratio of photometer time:

White 1 : Minus-Blue 11·7

denoting relative photochemical intensities of:

1 : ·085.

The effect of a cloud layer under a vertical sun seems to be less than in a temperate climate. The sunlight is intrinsically more actinic, and this superiority is not neutralized by filtration through clouds, for even under a densely clouded sky on Oct. 30th the photometer time did not rise above 6 secs. In the forest only readings for white light were obtained.

Photometric times in forest:

	In a sun-fleck	In deep shade
Nov. 6th	25 secs.	7 mins.

The average intensity for outside being taken as 1, these equal ·12 : ·0072, while their proportion to each other is 1 : ·06.

The tremendous difference made by the sun-flecks is clear, and they must have a manifest effect upon the ground flora, as they produce local increases of nearly 17 times the shade illumination. In order to give a better idea of what the above figures mean some similar observations taken at Reading are appended.

June 15th, 1915. Fine summer day, clear sky.

Photometer times:

	White	Minus-Blue
10.15 A.M. ...	3 secs.	50 secs.
11.0 A.M. ...	2 „	1 min.
12.0 NOON ...	3½ „	1 min. 35 secs.
12.30 P.M. ...	5 „	2 mins. 25 secs.
3.0 P.M. ...	5 „	1 min. 15 secs.

Average ratio of photometer time: White 1 : Minus-Blue 23·0.

Denoting relative intensities of: 1 : .044, compared with 1 : .085 in Rio. And the ratio of White intensity in England to the same in Rio is:

Rio 1 : England .66.

The Minus-blue intensity in England was therefore only .52 of the same light in Rio.

Thus the light at Rio was richer in photosynthetic rays, not only absolutely but also proportionately.

In the table given above it is interesting to note that the proportion of assimilatory light to total white light rises with the decline of the sun. The preponderance of yellow light in the afternoon is well known to photographers, but I doubt if the significance of the fact in the photosynthesis of vegetation has been properly estimated.

It is evident that the absence of minus-blue readings from inside the forest leaves us unable to form a judgment as to the full value of what light there is there. Such readings cannot be easily taken. The exposure time is so long that the sun moves quite appreciably (it takes from one hour to $1\frac{1}{2}$ hours, roughly) and all sorts of variations of lighting occur during the period. Of course knowing the average ratio between white and minus-blue intensities outside, we might calculate the theoretical minus-blue intensity inside, but the unexpected difference in the proportional constitution of the light in England and Rio raises the question whether such a proportion would be valid. Further consideration of the lighting of the forest floor renders it even more dubious. Outside of sun-flecks the amount of direct light reaching the ground flora is very small. The occlusion of almost all diffuse light from the sky by the high trees is evidenced by the remarkable darkening perceptible when the direct sunlight leaves the forest. Now that diffuse light which does reach shaded parts is reflected from surfaces within the forest, and chiefly from leaves. An attempt was made, based on these considerations, to analyse the lighting by spectroscopic means.

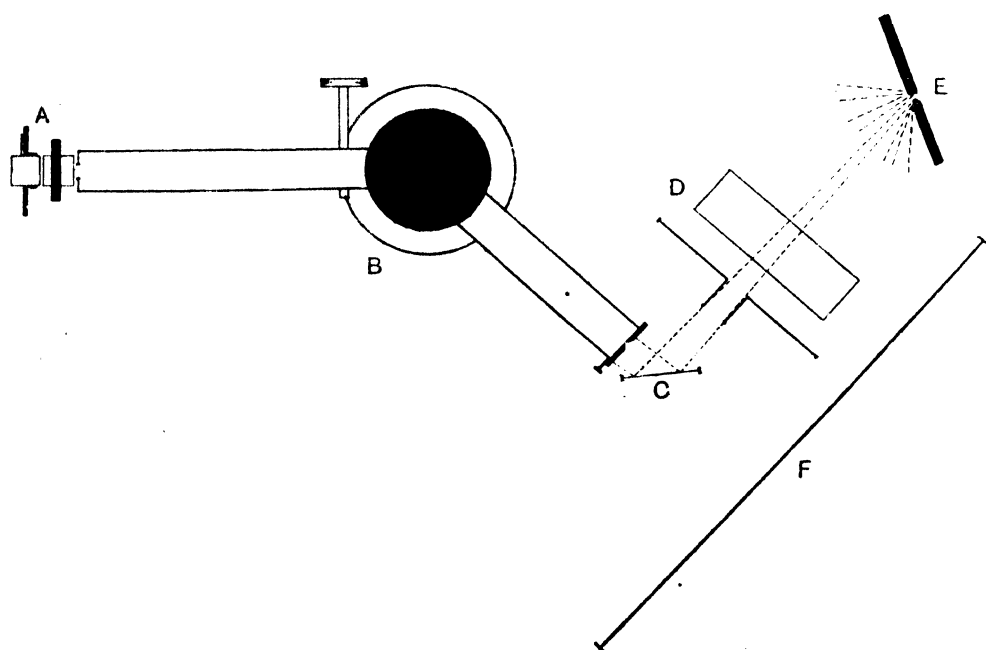
3. Spectroscopic Measures. The leaves of the undergrowth being the principal reflecting surfaces the obvious thing to do was to examine the relative intensity of cardinal points in the spectrum reflected from leaves of different shades of green, compared with pure white light, in order to obtain information as to the constitution of the diffuse light. The method of examination was this. Three common species were chosen, covering the extremes of leaf tint observed. These were species of *Ocotea*, *Sapindus* and *Artocarpus* (in order of density of coloration) and the apparatus shown in Fig. 5 was set up for their examination. It was necessary to work to an average in this way as not many species could be examined, and there is no generally prevailing tint.

The diagram is self-explanatory, except as to the actual method of measurement. This was effected by means of a polariser and rotating analyser

attached to the eyepiece of the spectrometer. With light of varying intensity the perception of the point of total extinction varies proportionately to the intensity, though not within wide limits, thus affording a means of direct measurement. A similar principle is embodied in the Heyde's exposure meter and in Hufner's spectrophotometer. As a standard of "Albido" several thicknesses of filter paper (Munktell's No. 2) did well.

The analyser prism was set to be parallel to the polariser with the pointer at zero of the scale, and the intensity was measured by the degrees of rotation to the extinction point. The dispersion of the spectrometer was sufficient to secure monochromatic fields of view.

Illumination was at first attempted with a heliostat fixed in the open,



A = Polarising Eyepiece. **B** = Spectroscope. **C** = Leaf, or other Surface.
D = Screen and Alum Trough. **E** = Electric Arc. **F** = Black Background.

FIG. 5. Plan of Apparatus employed for photometry of the spectra reflected from various surfaces

but this proving insufficiently reliable, the arrangement shown in the figure was adopted. The whole was placed in a dark room. A 200 c.p. arc with continuous current was then set up at about 60 cms. from the reflecting surface, an alum trough and pierced screen being interposed. The reflecting surface was 4 cms. from the slit, which was 1 mm. in width. The colours measured were:

Red, λ 6500.

Green, λ 5800.

Blue, λ 4800.

During the process of reading there is a noticeable increase in the amount

of red reflected from the leaf. This is doubtless a morbid phenomenon due to destruction of the chlorophyll under the brilliant light employed. On this account the readings should be taken as quickly as possible, and red examined first.

The final result of these measurements is given in Fig. 6. Two ways of regarding the results are necessary, viz. their intensities relative to the same colours in pure white light, and their intensities relative to each other. An inspection of the diagram will show that the absolute amount of diminution in reflection from a green surface is less than one would expect. Thus the average intensities relative to those in white light work out to:

Red, .883,

Green, .850,

Blue, .804

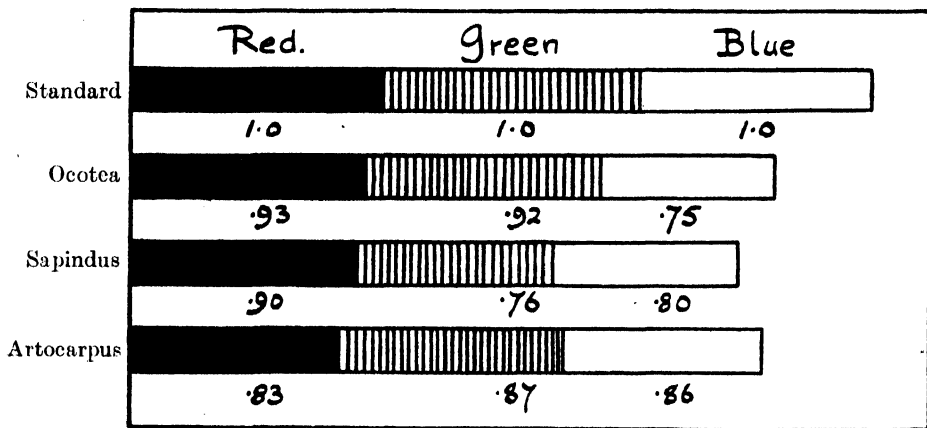


FIG. 6. Spectroscopic measures of light reflected from forest leaves. The total length of each "spectrum" represents the total amount of light of these three colours reflected in each case, and the sections show the relative amount of each separate colour. The figures represent the ratio of each segment to the corresponding colour-segment in the standard "spectrum" (taken from white filter-paper). It will be noticed that the highest aggregate ratio is in the red.

of the corresponding colours reflected from the white standard. On the average red is decreased less than the other colours, although the amount of red reflected decreases with greater intensity of leaf tint, while the blue proportion rises. This represents only the *proportional diminution* occurring in reflection from the leaves; the actual intensity is dependent, obviously, on the intensity in the white light. Turning to the leaf-reflected spectra themselves we find that the average intensities *inter se* are:

Red, 1.185,

Green, 1.175,

Blue, 1.0.

On both counts therefore red, not green or blue, is preponderant in the diffuse light of the forest. That this circumstance renders the diffuse, reflected light of more value for photosynthesis than might have been supposed from the photometer measures is evident.

Utilising this information we are now able to form an estimate of the

assimilatory lighting in the forest shade. By photometer we found that the actinic light in deep shade as compared with full, meridian sunlight was reduced from 1 to .0072. Now judging by the proportional luminosity of red and blue in the forest light, as found above, the assimilatory lighting only appears to be reduced from 1 to .0085. This may not seem much, but interpreted into photometer time it is worth consideration—thus:

Photometer time of minus-blue in deep shade:

A. Calculated from proportions obtaining in full sunlight = 1 hour 22 mins.

B. Calculated from true proportions in shade = 1 hour 9 mins.

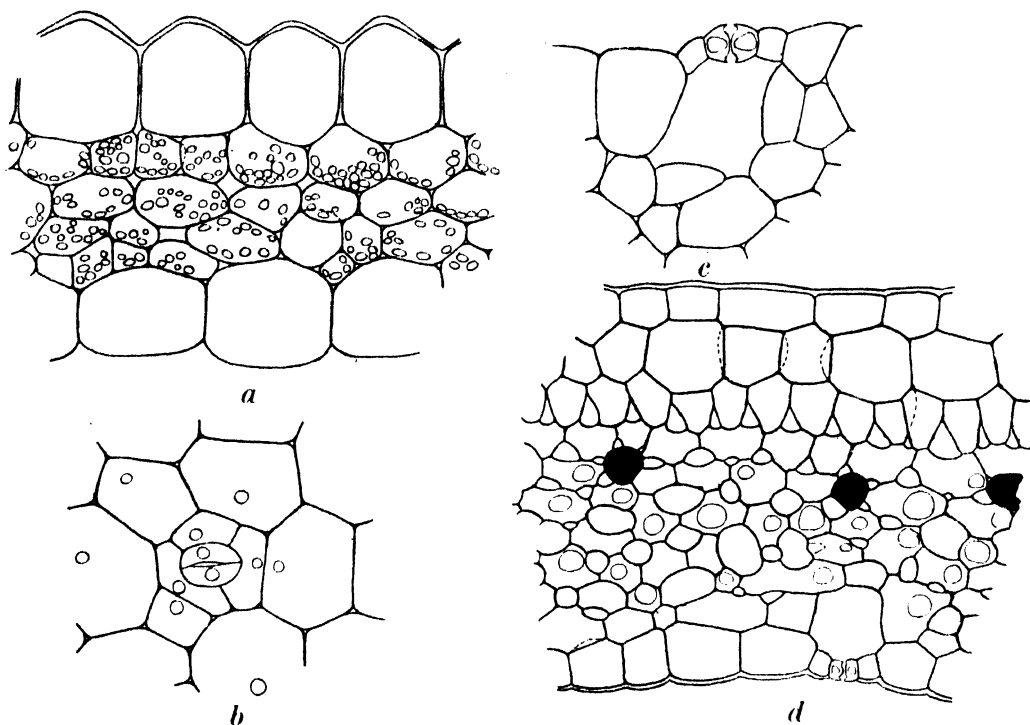


FIG. 7. *a*, *Physurus*, T.S. of leaf; *b*, *Physurus*, Stoma, surface view; *c*, *Physurus*, Stoma, sectional view; *d*, *Costus spicatus*, T.S. of leaf. All $\times 240$.

(b) THE LEAVES IN RELATION TO ILLUMINATION.

1. **Structure.** The morphological characters of the leaves have been dealt with to some extent under the transpiration question, but some further reference is needed here from the point of view of photosynthesis.

Broadly speaking the outstanding characters of the forest leaves are:

Their considerable size, and firm texture; their excellent mosaic; small number per individual plant; frequently perpendicular lamina; elongation at tip; lanceolate or ovate-cordate outline.

The cordate form is particularly common among climbers, and the basal auricles are extended well beyond the slender stems. As the leaves so often

point upwards, it is probable that this form facilitates drainage, particularly in channelled leaves.

Anatomically there are many peculiarities. The following are brief notes of the features of those species mentioned on page 38 in Part I; as seen in cross section.

Phyllanthus sp., Euphorbiaceae. Low herb. Fig. 7 *a*, *b* and *c*.

Epidermis on both sides swollen, aqueous. Upper surface with markedly pyramidal cells. Mesophyll quite undifferentiated, small interspaces; only 3-4 cells thick.

Tradescantia discolor, Commelinaceae. Low herb. Fig. 8 *e* and *j*.

(1) *Light form*, very large aqueous epidermis and hypoderm. Mesophyll four cells thick, formed of small parenchyma. Chloroplasts more in upper layer. Interspaces very small.

(2) *Shade form*. Epidermis as above, hypoderm only over mid-rib. Upper cells of mesophyll with tendency to V-shape.

Ficus rubiginosa, Moraceae. Tall shrub.

Epidermis large, flat, aqueous. Mesophyll extensive, no proper palisade. Upper layers small celled, compact, rich in chlorophyll, rest very lacunar.

Costus spicatus, Zingiberaceae. Tall herb. Fig. 7 *d*.

Epidermis normal; large celled colourless hypoderm above, probably aqueous. Mesophyll extensive, very lacunar, but upper layer formed of V-shaped cells with chloroplasts aggregated at their points.

Anthurium sp., Araceae. Low herb.

Epidermis swollen, aqueous, flat. Mesophyll very lacunar. Two upper layers of small cells, close, with abundant chlorophyll; rest practically colourless, but containing octahedral crystals. Radially elongated collecting cells round the veins.

Mapouria tristis, Rubiaceae. Shrub.

Epidermis large, good cuticle. Palisade of short fat cells, very chlorophyllose. Spongy mesophyll slight and very lacunar. Lowermost layer markedly chlorophyllose.

Echites peltatus, Apocynaceae. Shrub.

Epidermis strongly thickened, with labyrinthine ridges, giving velvety surface. Palisade of short, conical cells, loose. Spongy layer very scanty and loose.

Asterocaryum Airi, Palmaceae. Small tree. Fig. 8 *k*.

All cells small and thick walled. Strongly thickened epidermis and hypoderm, both of elongated cells, crossing at angle of 80°. Epidermis wears off in patches. Mesophyll undifferentiated.

Gomphia cuspidata, Ochnaceae. Shrub.

Epidermis normal. Palisade loose, short cells. Spongy tissue with V-shaped chlorophyllose collecting cells. Rest almost colourless.

Solanum auriculatum, Solanaceae. Shrub. Fig. 8 *g* and *h*.

Epidermal cells normal with labyrinthine ridges on surface. Upper epidermal cells occluded by brown deposit. Loose palisade. Spongy tissue almost non-existent, reduced to a few cells only in large empty space.

Mimosa sepiaria, Leguminosae. Tree. Fig. 8 f.

Epidermis strongly thickened. No hypoderm. Palisade very loose. Spongy mesophyll extremely tenuous but well supplied with chlorophyll.

Passiflora macrocarpa, Passifloraceae. Liane.

Epidermis large celled. Mesophyll only four cells thick, chlorophyll chiefly in upper and lower layers. Interspaces form large gaps in mesophyll.

Three facts emerge conspicuously in comparison of these notes. Firstly

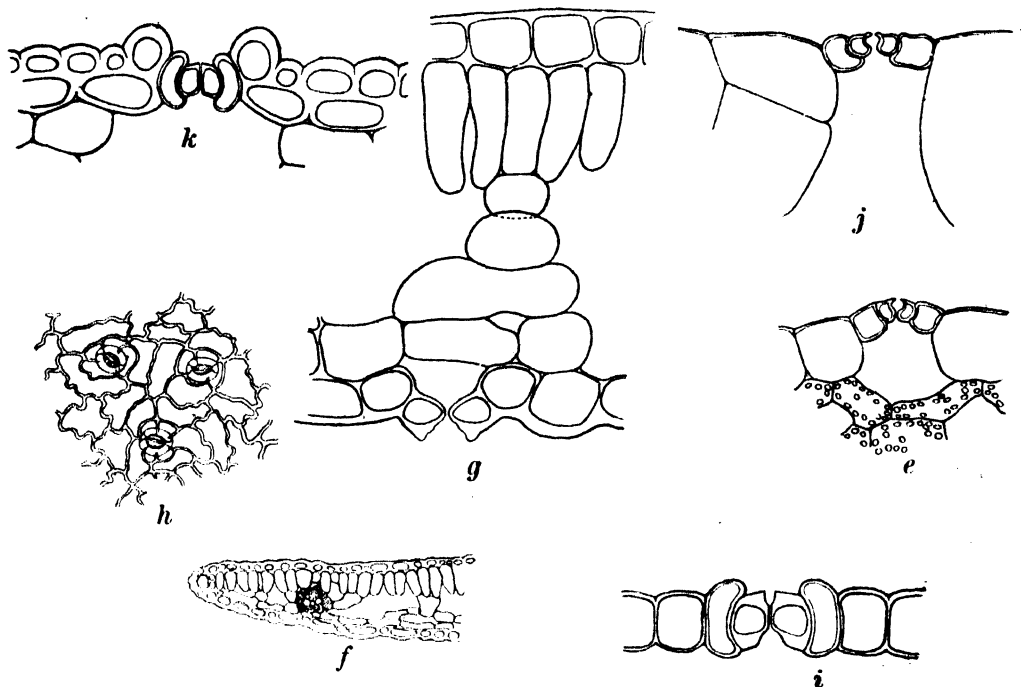


FIG. 8. e, *Tradescantia discolor*, Stoma, shade form, $\times 240$; j, *Tradescantia discolor*, Stoma, light form, $\times 240$; f, *Mimosa sepiaria*, T.S. of leaf, $\times 120$; g, *Solanum auriculatum*, T.S. of leaf, $\times 240$; h, *Solanum auriculatum*, Stoma, surface view, $\times 240$; i, *Solanum* sp., Stoma, sectional view, $\times 240$; k, *Asterocaryum Airi*, Stoma, sectional view, $\times 240$.

the prevalence of a water storage epidermis. This is just what might be anticipated from the conclusions of Part I, namely that the leaves were subject to sudden calls upon their transpiring power greater than their normal capacity allows for. The second is the slight differentiation of the mesophyll and the tendency to localize the chlorophyll near the leaf surface, owing no doubt to the slight penetration of the dim light; and the third is the occasional appearance of V-shaped assimilating cells, recalling those of the protonema in the moss *Schistostega*. In the latter case they have been interpreted as reflectors for concentrating the light upon the chloroplasts, which, as in these leaves,

are agglomerated at the point of the sub-conical cell. If the supposition is well-founded in the case of the moss, doubtless the same interpretation is here applicable. Contrasted with leaves taken from the Restinga bush on the shore, exposed to full insolation, the characteristics of the shade leaves appear to be more or less uniform.

The sun leaves contrast with them all in these points: Epidermis and hypoderm together, several layers thick, stout walled. Palisade very well marked, often 3 layers deep, spongy layer closer. Stouter cuticle and generally tougher texture.

In the mind of the careful observer there can be no doubt that the lanceolate, entire and glabrous leaf is the predominant type through all the families of the forest. This convergence can also be expressed statistically and yields a striking result. The prevalent surface, on the other hand, is a more subtle thing to estimate, for so much depends on opinion; but, in spite of some marked exceptions, smooth surfaces are the rule, many polished, and not a few glaucous. The exceptions are the hairy and velvety leaves. That these dry quicker after wetting there can be no doubt—their surface is much greater—but whether they obtain any marked advantage in this, especially regarding freedom from epiphyllae, requires exact investigation, not mere expression of opinion. The similarity of foliage in plants of such diverse affinities can only be explained on physiological grounds, in other words a convergence towards a common form best suited to the environment. The convergence is so close that in the barren condition it is next to impossible to identify the genus of a plant of the undergrowth, and practice is needed even to guess the family.

Plants of the lower layers have remarkably few leaves as a rule, and these tend to be placed in a few planes or borne in tufts at the ends of branches otherwise bare. Thus the bushes are very “leggy” though dense at the actual level of the leaves. Judging from the accounts given by earlier writers, there seems to be a prevalent idea that the leaves in the shade of jungles reach abnormal dimensions, and this is supported by experiments made elsewhere on the effect of shading on leaf size. Scott-Elliot however (1891) by observation showed that in *Helianthus* the contrary was the case. Leaves, he says, in moist air appear to be narrower than leaves in dry air, and from this have smaller surface. Sunlight produces larger leaves than shade on plants of the same species, and he goes further and maintains that enlarged leaves are characteristic of heliophytes as a whole. He quotes from Sorauer (*Bot. Zeitung*. Bd. ix. Pt I, 1878) to the effect that leaves become actually as well as relatively longer in sunshine.

The truth of these observations was tested by a series of comparative measurements.

2. Dimensions and Variation. As a basis for comparison, measurements were made of the length and breadth of 1000 leaves, taken from 100 species, of which fifty were pronounced sciophytes, and fifty equally pro-

nounced heliophytes. The predominance of simple, petiolate leaves made accurate comparison possible. Ten leaves were taken from each species, withered or immature ones being avoided. The ratio of length to breadth was found for every case and averages taken both for all shade and all sun leaves as individuals, and also for the leaves of each species together¹. By this means some idea of the relative variability of the species may be gained. It is hardly to be expected that any constant of variation should exist over the entire population of a habitat, but something of the sort may probably exist for each species; indeed biometrical examination of the range of variation in species may be regarded as promising to lead to a much clearer conception of that disputable unit. The general results are shown in Fig. 9, in which one portion deals with the ratios of all the leaves, another with the specific averages. It will be seen that in both cases the curves are of the same general type.

In Fig. 9, curve A, which represents the sun leaves, is much steeper and simpler than curve B, the shade leaves. The range of ratios starts from almost the same point, i.e.

$$\frac{\text{Length}}{\text{Breadth}} = .7,$$

but the sun curve culminates rapidly at 1.7 (57 individuals) and stops at ratio 5, while the shade curve has two summits rather widely separated, one at ratio 2 (27 cases), the other at 2.8 (27 cases) and runs up to ratio 8.5 (neglecting one anomalous case of a ratio 13.5).

The average ratio for sun leaves is 1.75, very close to the summit of the curve; that for shade leaves 3.03 (1.73 times as much) which is beyond either summit of that curve. In other words the ratio of length to breadth in shade leaves is greater (in the above proportion) than in sun leaves. The latter also appear to be more stable in type, with a simpler variation curve than the former. The ratio does not however convey any information as to actual sizes.

The average breadth of the sun leaves was 4.93 cms., and their average length was 8.63 cms., giving a rectangular area of 41.8 sq. cms.

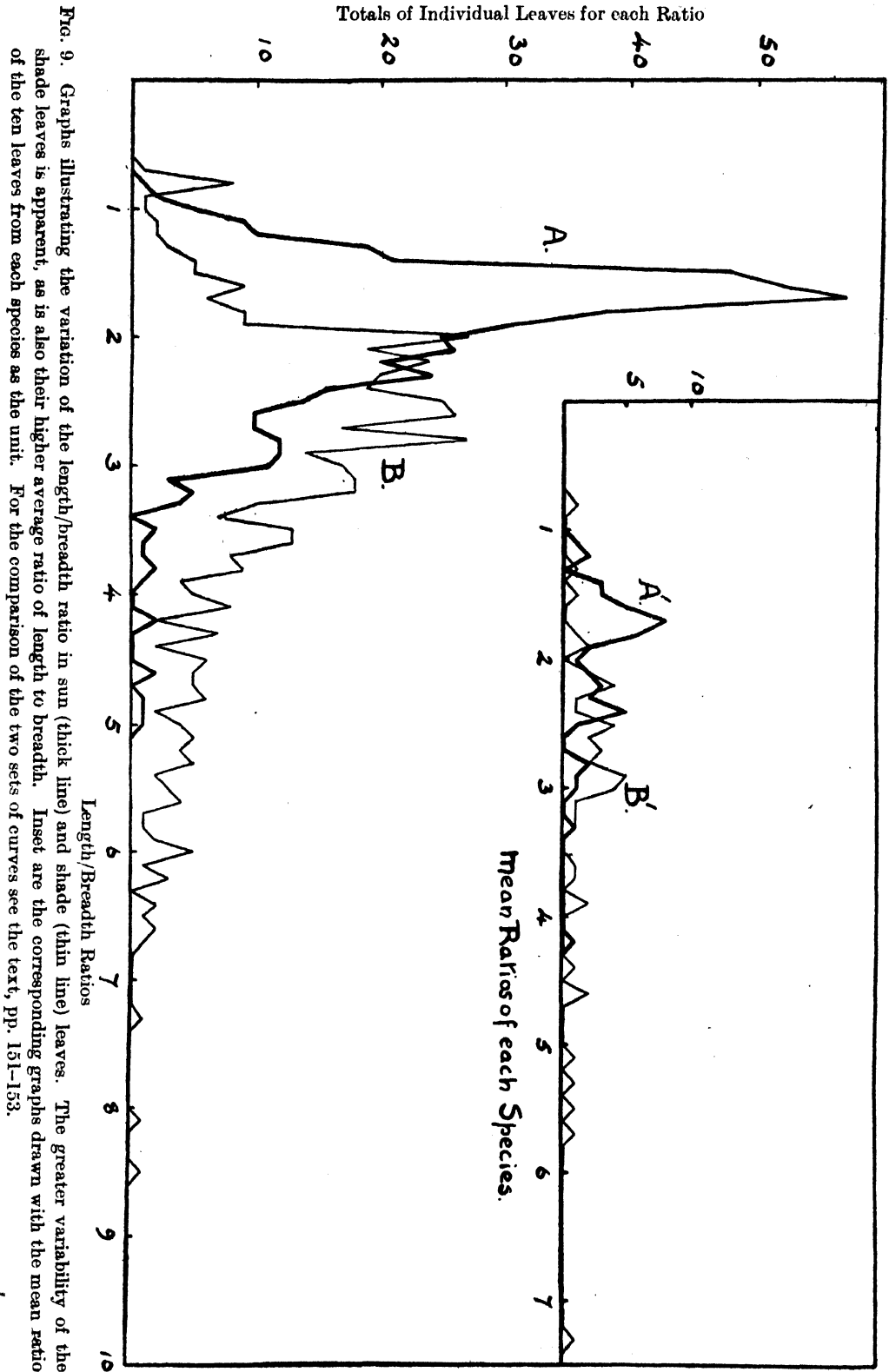
The average breadth of the shade leaves was 3.54 cms., and their average length was 10.72 cms., giving a rectangular area of 37.9 sq. cms.

The length is more variable in the shade leaves than in the sun, but the breadth is more variable in the sun leaves, in approximately the same proportion, so that altogether the actual areas appear to be nearly the same, the shade leaf being on the average longer and narrower.

The length/breadth ratio in sun leaves varies from .8 to 5.0. Range = 4.2.

In shade leaves it varies from .7 to 8.5. Range = 7.8 or 1.86 times as much. The variation in form is thus 1.86 times greater in shade than in sun leaves. In all likelihood the sun plants are under much more uniform conditions than those of the shade, exposed as they are to many accidents of

¹ I am much indebted to my wife for carrying out the laborious business of working out the ratios and constructing these graphs.



circumstance in lighting. Turning now to the species as a unit, we find as before that the curve of the sun ratios culminates at 1.7, that of the shade at 2.2 and 2.9. The range of variation is however smaller:

Sun = 1.0-4.3. Range = 3.3.

Shade = 0.8-7.3. Range = 6.5 = 1.97 times as much.

In this case the proportionate variability of the shade leaves is slightly greater (1.97 : 1.86).

Some species in both habitats are obviously much more plastic than others. The following is the range of variation within single species:

Sun plants: smallest variation 0.15.

greatest ,, 1.70. Difference 1.55,

Shade plants: smallest variation 0.2

greatest ,, 3.2. Difference 3.0,

or an extreme range of specific variation of 1.93 times as much.

The *average* range of specific variation within each habitat was, on the other hand:

(A) Sun plants: 0.63.

(B) Shade plants: 1.17, or 1.86 times as much.

In every case the balance of variability is heavily on the side of the shade plants.

The range of variation for the leaves individually was, it will be recalled:

(C) Sun leaves: 4.2,

(D) Shade leaves: 7.8,

which is also 1.86 times as much.

This is rather a suggestive result. $A : B = C : D$, but also $A : C = B : D$; that is to say it appears from the foregoing figures, relevant to two contrasted habitats, that the average variation of leaf-size in the separate species of a habitat is a function of the extreme variation of leaf-size in the plants of the habitat as a whole. In simpler language, the greater the total range of leaf-size in any given habitat, the greater the intrinsic variability of leaf in the species there occurring. In interpreting such a maxim it is important however to discern that the term "habitat" must in this connection be taken as defined by climatic, not edaphic factors. Much interest might no doubt be extracted from the comparison, in a similar manner, of organs directly under the influence of edaphic factors. In regard to the relative constancy of size in the two cases dealt with above, it is worth notice that:

Among sun leaves 11.4 per cent. fell on one ratio, viz. 1.7.

Among shade leaves the greatest number falling on a single ratio was 5.4 per cent., viz. on 2 and 2.8.

I have little doubt that the elongated apices described by Stahl (1893) as "drip-tips" find a simple and unteleological explanation in the general elongation which is here shown to be well marked among shade leaves.

As before mentioned under this heading the arithmetical investigation of

specific characters, especially such as lend themselves to easy measurement, like those I have dealt with, should be urged as the key to a much closer analysis of biological units than can ever be possible by descriptive methods alone.

3. **Red Coloration in Young Foliage.** One of the minor problems associated with the study of shade vegetation is that of the frequent red coloration of young leaves which is a feature of the more pronounced sciophytes, a peculiarity rendered all the more obscure by the occurrence of similar colours in the young leaves of some extreme heliophytes. It is not confined to Angiosperms, but it is common among the ferns, and moreover persists under cultural conditions. An exactly similar appearance may be seen during the vernalization of undergrowth in this country, and the author has noticed it conspicuously in coppiced hornbeam in the shade of standard oaks, and also in hawthorn. The explanation hitherto offered is that this colour is concerned with the more effective absorption of light, an explanation based solely on analogy with the Rhodophyceae, not on experimental grounds. It is difficult to apply this hypothesis to the heliophytes. The latter were shown by Keeble (1895) to reflect heat better if coloured red than green, which seems to give reasonable ground for regarding that case at least as protective. The sciophytes are obviously in a different category; they stand in need of no protection, but they are likely to require ameliorated conditions of assimilation. It does not appear to have been stated clearly anywhere that the two colorations are absolutely distinct; that in the heliophytes is a sap coloration of anthocyanin, acting as a shield against the sun, that of the sciophyte is a plastid coloration of erythrophyll. It is on this ground that its interpretation as an augmentor of assimilation is possible. We have seen, however, that red and not green light is preponderant in the forest, so that the differential absorption presumed to exist would not be accomplished by the development of red colouring matter. Protection being excluded, it only remains to suppose that the red leaves are specialized in respect of respiration. Reduced respiration would unquestionably increase their assimilatory efficiency. This point has been tested, though not exhaustively. Red young leaves, and leaves which had just gained their normal colour were selected from a plant of *Eugenia* (*E. guabiju* Bg.) and enclosed in glass vessels with glycerine manometers attached, and tubes containing potash to absorb the CO_2 given off. The comparative rise in the glycerine column is shown in the graph, Fig. 10. It is only possible to continue readings with leaves removed from their parent plants for a short time, otherwise a pathological increase in respiration becomes inevitable. In the diagram *A* is the graph of the red leaves, *B* of the green leaves, and it will readily be seen that the respiration of the former is greater than that of the latter, the manometer tubes having exactly the same bore. This fact makes the red coloration appear as a disadvantage to a shade plant, inasmuch as increase of respiration implies decreased assimilatory efficiency.

It is clear that some other cause must be sought to account for this phenomenon, which remains for the present an unsolved puzzle.

(c) RESPIRATION.

1. **Respiration Measurements.** Supplementary to the question of the relative respiratory powers of red and green young leaves acting in their normal environment, is the further topic of the behaviour of normal sun and

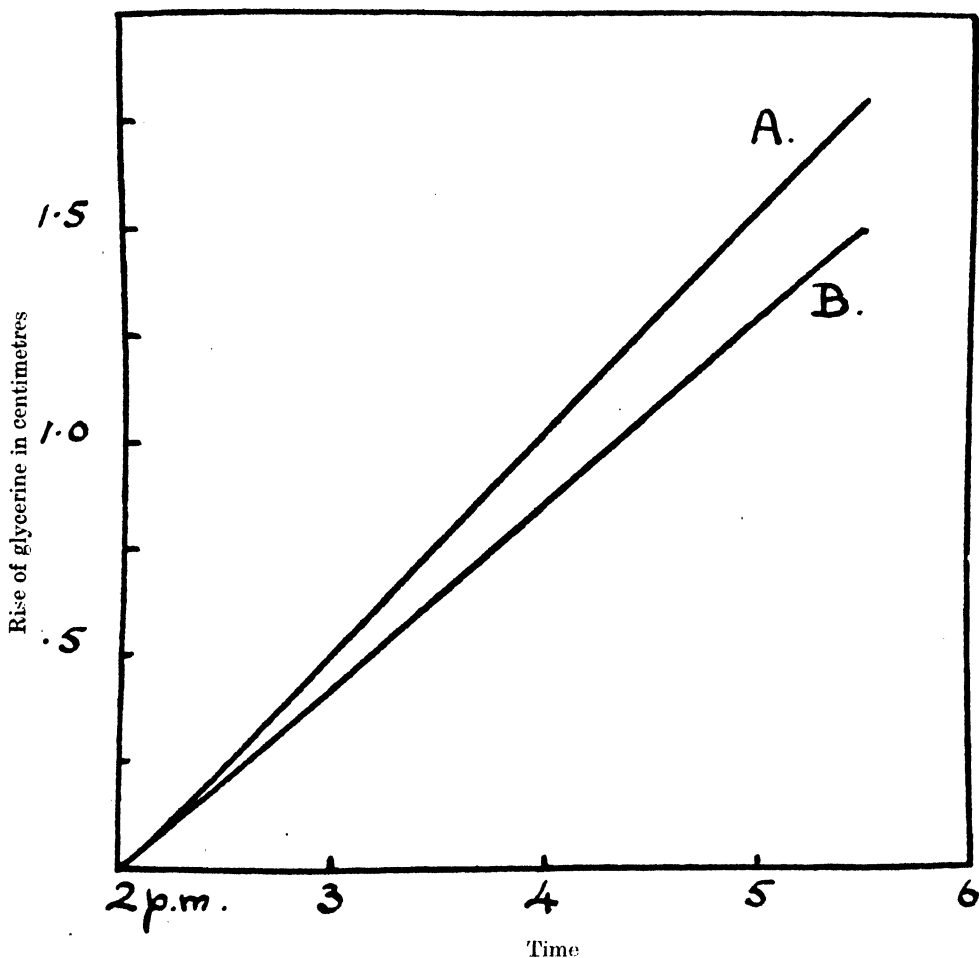


FIG. 10. Respiration of equal weights of shade leaves, red coloured (upper line) and green coloured (lower line) of the same species of *Eugenia* from the forest undergrowth. Measured by the rise of glycerine, the evolved CO_2 being absorbed by potash.

shade leaves comparatively to each other in this respect. The only apparatus available for measurement was crude, depending on the measurement of a rise in a column of mercury, as in the respirometers commonly used with germinating seeds, but care was taken to minimise the inherent imperfection of such a method. Sun leaves from a plant of *Psychotria* in the gardens and

shade leaves from a species of *Mapouria* (*M. tristis* v. M.) were compared together respiring in the sun.

Nov. 29th. In sun. Radiation temperature at noon (black bulb in vacuo) 45° C.

Exposure for 22 hours, from noon on the 29th till 10 a.m. on the 30th.

Weight of leaves used:

Sun (*Psychotria*) .641 gm.

Shade (*Mapouria*) .426 gm.

of approximately the same size and stage of development.

During the above period the CO₂ evolved was:

Sun leaves: 1.48 c.c. per gm. of leaf,

Shade leaves: 3.28 c.c. per gm. of leaf,

or 2.2 times as much as the sun leaves. The shade leaves eventually blackened and died, although in a moist chamber, so that the result is probably pathological. It does not seem possible to get a fair comparison of their behaviour in the sun, except in so far that the shade leaf is more sensitive to exposure than the sun leaf. Several reasons may contribute to this. The chlorophyll of the shade leaf is more exposed, the colourless tissues being less developed and the cuticle thinner. Now increased "chlorovaporisation" (to use Van Tieghem's term) should lead to greater cooling, if the water supply were adequate, which we have seen in Part I is not the case with the shade leaf. It cannot take in water up to its total diffusive capacity, which is in any case less than that of sun leaves, so that the cooling possible by evaporation is of very limited extent. As the leaves are in CO₂-free and very moist air, more light energy is converted into heat than normally, leading to a fatal rise of temperature in the chloroplasts.

These results, though imperfect, raise the question of the general validity of the belief that respiration is reduced in shade plants. If the respiration is really high, then some effect of it in raising the CO₂ percentage of the air in the dense masses of forest vegetation might be perceptible, especially at the end of the night. It seems possible that the extent of decay would produce a rather unusually high percentage in any case, but only the amount contributed by respiration would be expected to show a diurnal fluctuation.

2. Carbon Dioxide in the Forest Air. Two estimations of the CO₂ were made by Pettenkofer's method, one in the evening and one in the morning. A five litre flask was fitted with a bung through which passed the tube of a 200 c.c. stoppered funnel. The flask was filled with water and 150 c.c. of a saturated solution of baryta was introduced into the funnel and the flask bunged. It was then removed to the forest and the water poured out slowly, the flask being held at 1½ metres above the ground at the same spot each time, among dense, shrubby undergrowth. The baryta was then run into the flask from the funnel and shaken about for 10–15 mins. The flask was inverted, the stop cock of the funnel opened, and as much baryta as possible

allowed to run back into the funnel. For this purpose it is essential to employ a funnel with a wide bore tube and tap, otherwise the baryta will not run back. Aliquot parts may then be pipetted off from the funnel and titrated against equal quantities of the original solution. This method is easy to carry out and seems suitable for such experiments.

The acid employed was sulphuric, of such strength that 1 c.c. = .000614 gm. or .312 c.c. of CO₂.

Experiment I. Dec. 29th. Humidity high, no rain.

Radiation temperature at noon, 50° C.

Evening, 5.30 p.m. Before sunset; no wind.

CO₂ in 5000 c.c. air neutralized the baryta equivalent of 24.0 c.c. of acid = .14 c.c. of CO₂ per cent. of air at N.T.P.

Experiment II. Dec. 30th. Morning, 6.30, 2 hours after sunrise. The night was fine, warm and open; no rain, no wind.

CO₂ in 5000 c.c. air neutralized the baryta equivalent of 59.25 c.c. of acid = .34 c.c. of CO₂ per cent. of air at N.T.P.

These are decidedly supernormal percentages, and it is obvious that in the absence of wind the night respiration has a very marked effect on the amount present in the forest air. A certain amount of work has already been done on the effect on plants of high percentages of CO₂; particularly Brown and Escombe (1902), Demoussy (1904) and Farmer and Chandler (1902). These investigations agree that the surface of the plant in high percentages of CO₂ (.1–.5 per cent.) undergoes limitation, that flowering is inhibited, and that the leaves show abundant starch; while Farmer and Chandler remark increased intercellular space. In all these particulars the vegetation of the forest undergrowth affords the recognizable characters of a carbon dioxide vegetation. In regard to the first point we have shown previously that the average leaf *area* in the forest undergrowth is only equal to the average of the exterior vegetation, while other observers have declared that shading increases leaf-size, other factors being equal. In all probability this apparent exception may be charged upon the high percentage of CO₂ present and its limiting action, independently of shade effects pure and simple.

Sufficient is known now of this factor to enable one to see definitely that in the forest the amount of light, not the amount of carbon dioxide, is the limiting factor in assimilation, thus constituting a reversal of the ordinary state of affairs. This throws into relief the importance of sun-flecks to the undergrowth, a fact previously urged in this work, and supported by the observations of Wilhelm Plester (1912), that a shade leaf brought into greater light assimilates more than an equivalent photophilous leaf, that is to say it is more sensitive to comparatively small changes of illumination.

Whatever may have been the general condition of the atmosphere in carboniferous times, it seems legitimate to conclude that the undergrowth of its forests must have lived in an atmosphere rather richer in CO₂ than the

contemporary normal, so that conclusions drawn from preserved microscopic structure should only with reserve be extended to apply to the atmosphere of the period as a whole, exterior to the forest.

3. Observations on Assimilation. Under the last heading it was shown that the increased amount of CO_2 in the forest air turns the light into the limiting factor. This enables it to be more completely used in assimilation than is possible among mesophytes and moreover renders its spectroscopic composition of more importance. Under ordinary circumstances it is well known that diffuse light may be quite sufficient to carry on photosynthesis, direct sunlight only serving to heat up the leaf. It was shown by Brown and Eescombe (1905) that of the energy flowing into a leaf in the form of light only .27-1.66 per cent. is used for photosynthesis and from 9.67 to 60.03 per cent. for transpiration (by raising the temperature). Our photometric measures of the forest light show, however, fractions of full sunlight strength ranging well below the smallest of these, so that a lack of light is certain. According to the above investigators, about 85 per cent. of the light absorbed by a leaf is absorbed by the colourless tissues. Hence we perceive the need for very thin and transparent leaves in the undergrowth, reducing the needless light absorption to a minimum. This is not only necessary to allow access of the maximum of light to chlorophyll in all parts of the mesophyll, but also to avoid heating, due to the absorption of light by colourless tissues, which under conditions of restricted transpiration can only lead to an increase of respiration. Hence mere reduction of non-effective light absorption, apart from any increase in the effective absorption which might be inferred in these leaves, will tend to bring the fraction $\frac{\text{Assimilation}}{\text{Respiration}}$ to a maximum.

This seems to be the key to the reduction in leaf thickness and also perhaps to the adoption of erythrophyll colouring in some young foliage. It has been shown by Plester (1912) that the red screen of anthocyan in leaves of *Catalpa purpurea* "provokes" a high chlorophyll content, with a consequent increase in the effective light absorption. Possibly the erythrophyll plays here a similar part.

That assimilation does proceed effectively under the prevailing conditions is proven by the abundance of starch in the leaves, even in those from the extremest shade, as shown both by Sachs's iodine test and by microscopical examination. This indicates the existence of a balance of adjustment between light-ration and CO_2 -ration quite foreign to the nature of mesophytes.

Finally, an attempt was made to ascertain if the chlorophyll of an extreme sciophyte was qualitatively different in regard to light absorption from that of ordinary mesophytes. This was tried with *Anchietia*, a violaceous plant from the deepest shade, by illuminating a leaf enclosed in a small box, with a solar spectrum, projected through a slit in the underside of the box by a Ziess "Spektralobjectiv," the whole being mounted on the mechanical stage

of the microscope to enable leaf and spectrum to be registered again on one another, after the leaf had been detached from its plant and "developed" with iodine. The idea seemed promising, but the result was inconclusive owing to insufficient exposure, and time prevented the repetition of the experiment. It is an investigation probably worth following up, for such a differential adjustment of the chlorophyll is not unlikely in the plants of the shadiest depths.

GENERAL SUMMARY.

1. PHYSIOLOGICAL STATUS OF THE UNDERGROWTH: TRANSPIRATION.

(PART I. SECTION A¹.)

1. The forests included within the scope of this survey are the sub-montane forests of the coastal plain and the Serra do Mar, in the States of Rio de Janeiro and São Paulo, South Brazil (page 5).

2. These forests are typical rain-forests, enjoying a thoroughly tropical climate, with constant high temperatures, high precipitation (which shows a marked seasonal fluctuation), constant high humidity, and strong solar radiation (page 11).

3. The objects in view were the study of the factors of moisture and illumination in the interior of the forest, and their influence on the undergrowth (page 16).

4. Records are presented of the humidities and temperatures occurring in the forest and the conclusion is reached that the climatic factors affecting the lower layers of the forest are almost diametrically opposite to those influencing the upper layers, though the edaphic conditions are the same for both. The shrub layer seems to divide the forest climatically into two distinct strata. The lower of these is the principal object of this study (page 23).

5. Some measures of transpiration in the forest are presented (page 24). A comparison of the various types of leaves employed, with reference to their transpiration capacity, is elaborated; and the general question of the presence of any adaptations designed to increase transpiration decided in the negative; some experiments performed in England were utilized for comparison (page 29).

6. A new hypothesis of the biological significance of nyctitropism is submitted (page 27).

7. It is shown that, despite the very high humidity, a certain amount of xeromorphy is traceable in the leaves, and this is explained by the proved coincidence of two factors:

(A) The theoretical diffusion capacity of the leaves is excessively large compared with their habitual transpiration, while the passage of sun-flecks across the leaves is capable of sharply lowering the environing humidity and

¹ See this JOURNAL, 7, p. 5.

consequently of causing sudden increases in evaporation. The prevalence of a water storing epidermis is a natural effect of this phenomenon.

(B) The xylem supply in the leaf petioles is inadequate to carry water for more than a small fraction of the total possible evaporation from the stomata. It appears only to be developed proportionately to the small habitual transpiration in the shade, and is very much lower than in the sun plants examined for comparison.

This last observation (B) suggests that the water supply from the roots must be restricted, for if this were not the case an increase of xylem supply, correlated with (A), might have been anticipated (page 35).

8. In spite of the very slight foliar transpiration, no excretion of fluid water has been observed, so that root absorption may actually be low. This does not exclude the possibility of considerable quantities of water being absorbed and immobilized in the plant by (a) the predominant and continuous elastic growth, (b) water storage to meet sudden evaporation, (c) starch formation in photosynthesis, (d) return to the roots through the phloem.

Occlusion of water will stimulate a current in the hadrome independently of evaporation, just as the first swelling of buds during the vernal sap flow, previous to the commencement of transpiration proper (page 49).

9. Lastly an examination has been made of the mineral salts absorbed by the forest undergrowth. The content of ash proved to be as high or higher than in sun plants in the same neighbourhood. The evidence is therefore against the supposed connection between salt absorption and transpiration. Apart from the possibilities mentioned in (8) above, it must be remembered that the amount of water present in the tissues of these plants is higher and the amount of carbonaceous material lower than in mesophytes. The plant thus resembles a dilute solution, in which simple diffusion of salts along the vasal water columns and through the cell walls may proceed with less than normal resistance.

The author inclines however to the opinion that the demands of rapid and continuous elastic growth are the most influential factor in replacing the ordinary pull of foliar transpiration (page 50).

(PART I. SECTION B.)

1. The soil is shallow and pervious. It is derived from an impervious and peculiar sub-soil, which appears to be of the nature of laterite, a sub-aerial deposit (page 122).

2. The average water content of the soils is low, up to 10 per cent. of the net weight of the soil; and the mechanical analysis shows a preponderance of coarse particles which easily explains this (page 123).

3. Examination of the hygroscopicity of the soil leads to the conclusion

that no water is held hygroscopically in the wet soil and that this property is only shown by soil when air-dry (page 124).

4. The saturation capacity of the forest soil is about 40 per cent. of the weight of dry soil, but the average water content is only 20–25 per cent. of the saturation capacity, so that the water content may sometimes become a limiting factor to growth (page 127).

5. It was observed that a position on the hill top, the soil of which was drier before rain, and had a lower absorption capacity than the soil of a station at the hill foot, yet received greater benefit, i.e. more soil water, from an equal amount of rainfall. This led to an examination of the relative amounts of rain reaching the soil through the canopy of foliage. This proved to be greater in the former case. Some general considerations are appended tending to show that this factor, namely the amount of rain which, in any given association, actually finds its way to the soil (rainfall efficiency), is one of widespread ecological importance (page 130).

6. Analysis of the soil shows it to be very deficient in mineral nutriment, and particularly in calcium carbonate. The biological effect of the absence of this salt, in preventing nitrification and the liberation of the nitrogen of the humus, is pointed out (page 134).

7. The estimation of humus is rendered difficult by the presence of a high percentage (5.25 per cent.) of ferric oxide, which is itself reduced by the customary ignition for determining the humus. This is avoided by dissolving the humus in ammonia. The amount of humus is small, only about 3 per cent. of the dry soil, but compared with the exceedingly small quantities of soluble mineral salts, it is sufficient to indicate that the soil is a "geloid" one. As is frequently the case where only small quantities of soluble humus are present its nitrogen content is high (8.9 per cent. of the humus, or .225 per cent. of the dry soil), but it is shown that it is probable that this is only in small part available for the plants (page 135).

8. By a system of differential water extraction it was shown that the solution withdrawn at once from a soil which has been saturated with water after having been dried is about 1.5 times as strong as the solution withdrawn from the same soil after it has stood for some time in a saturated condition. This is attributed to re-adsorption of the mineral salts from the soil water by the hydrated colloids. The bearing of this observation on the deterioration of the soil after clearing of the forest is discussed (page 136).

9. The soil is shown to contain unsaturated humus and this is probably the cause of the restricted root absorption indicated in Part I. Associated with the occurrence of unsaturated humus is the abundance of mycorrhiza, which are very prevalent among the plants of the forest undergrowth. Fungi must play a large part in making up the nitrogen deficiencies of the soil, and it is perhaps not too much to expect that all these sciophytes will one day prove to be provided with mycorrhiza (page 139).

2. PHYSIOLOGICAL STATUS OF THE UNDERGROWTH: ASSIMILATION. (PART II.)

1. Photometric measures of the light intensities in full sunlight and in the forest were compared. In the former case use was made of a special yellow gelatine filter which cuts out all the actinic rays beyond λ 5200, to enable a truer estimate of the assimilatory rays to be made. Comparison was also made with sunlight in the English summer, with the result that the sunlight in Rio proved to be proportionately richer in photosynthetic rays.

The white light in the forest is shown to be enormously diminished and the effect of sun-flecks is definitely exhibited, but direct measures of the photosynthetic lighting were impracticable (page 142).

2. To avoid the above difficulty, the analysis of the forest illumination by spectroscopic means was attempted (page 144).

3. Three points of the spectrum, reflected from picked types of forest leaves, were analysed photometrically. Comparison showed that red was the colour reflected with least diminution. As by far the greater proportion of the light in the obscure depths of the forest is derived from foliar reflecting surfaces, it follows that red is the predominant colour in the shade. On the basis of this determined superiority of red to green and blue in these measures, it is possible to calculate the theoretical value of the *assimilatory* lighting in the shade, which is, on these premises, higher than simple proportion based on the outside measures would lead one to expect (page 146).

4. Notes on the structure of the leaves of some of the prominent sciophytes are given. Three features are conspicuous—water storing epidermis, reduced and undifferentiated mesophyll, and the occasional appearances of epidermal papillae and also V-cells in the mesophyll, interpretable as illumination devices. In conjunction with this, the observation in Part I, Section A that the shade leaves, compared mass for mass with sun leaves, have a proportionately greater amount of intercellular space is interesting (page 148).

5. A statistical investigation of the leaves of sun and shade plants has shown that the average of leaf-areas is closely similar in both cases, but that the shade leaves are decidedly longer and narrower than the sun leaves. The balance of variability is heavily on the side of the shade plants. On the basis of these comparisons it is enunciated as a theory, that the average variation of leaf-size among the separate species of a climatically delimited habitat is a function of the extreme range of variation of leaf-size found within the habitat (page 150).

6. Comparison of the red young foliage, produced by many undergrowth plants, with green young foliage has shown that the former have a higher rate of respiration. Protection against transpiration or insolation being excluded this result leaves it problematic what advantage the colour confers. Red being predominant in the light red leaves may perhaps absorb less needless light than green leaves, but this advantage is not shown by a diminished

respiration. It remains to be seen whether perhaps they have an abnormally high chlorophyll content masked by the red colour, which might favourably affect their assimilation (page 154).

7. An abnormally high percentage of CO_2 has been shown to exist in the forest, increasing largely during the night. This is reflected in the leaf structure of the plants, corroborating experimental work previously done on this question. It suggests the enquiry whether the respiration of sciophytes is really reduced under natural conditions, or whether assimilation is not aided by some abnormal sensitization of the chlorophyll (page 156).

8. Light is here the limiting factor of assimilation. Many factors appear to assist in the difficult task of nourishment, on a poor soil and immersed in gloom. Of these factors, mycorrhiza and the large absorptive capacity of the leaves deserve emphasis. Adaptations designed to assist transpiration have not been found, and the plants seem to thrive satisfactorily without them (page 158).

APPENDIX.

DESCRIPTIVE ECOLOGY OF THE FOREST.

1. **Floristic.** It is generally regarded as indispensable, even in the purest physiological ecology, to take into consideration the floristic composition of the vegetation dealt with. The list which follows makes no pretence of completeness, an aim which would indeed far transcend the limits of this work, since the flora of the state of Rio de Janeiro has some claim to be considered the richest in the world. It is estimated that the total population of vascular plants of the Federal Area round the city of Rio (in size approximating to the County of Middlesex) embraces not less than 10,000 species. Although this is but a rough calculation it serves to show the quality of the forest country we have dealt with.

Through the whole list there runs a dominant element of woody plants, emphasizing firstly the continuity of the growing season in this climate and secondly the importance of mechanical strength in the intense struggle for existence carried on in the forest. Herbs are not plentiful. The ground flora, which is chiefly composed of them, is sparse and open, with wide interspaces of bare soil, and it is only where the fall of some ancient tree of the forest canopy makes an open space that the herbs compete seriously with the shrubs, or form dense masses. Nor are Cryptogams much more conspicuous: ground-living mosses are largely precluded by the carpet of dead leaves, and the Ferns and Lycopods (especially *Selaginella*) frequent the rocky spots, particularly of course where there is dripping or trickling water.

In a general sense, Leguminosae may be called the principal family. They form a large proportion of the high forest, and as they are nearly all nyctitropic they are important physiognomically. Among the undershrubs Rubiaceae and Piperaceae are the most important, *Piper* itself, in various species, being

represented by a vast number of individuals. They produce, of course, the inconspicuous flowers characteristic of most undergrowth plants; flowers which are of small size even when they are polymeric, as in Anonaceae. Reduction of floral parts and size is so general in this environment, that it cannot but urge upon the observer the conclusion that the Piperaceae, its most characteristic family, are extremely likely to partake of the same effects, as they share in the causes which have brought them about.

Ecological conditions have been largely overlooked in morphological enquiry. It is difficult to believe that, in general, primitive organisms will be found in a highly specialized environment, and such the forest undergrowth seems to be. It is not a likely habitat for primitive forms, if we take into account the immense amount of evolution which has gone on in it, and the keen competition for the somewhat peculiar alimentation.

Possibly one might go further and suggest that nutritive causes may be at the back of all floral reduction in Angiosperms, the specialization to insect visits having simply determined the lines along which reduction has taken place. In such a view insect visits would operate purely as a selective influence during the progress of reduction, itself traceable directly to internal metabolic factors, under the influence, possibly, of the ecological conditions of the habitat. From this viewpoint economy of the densely protoplasmic, reproductive material, not insect adaptation, appears as the principal end in floral evolution. Certain families have undoubtedly found the most comprehensive reduction to be possible by the abandonment of insect specialization altogether and a secondary assumption of anemophily. Where mesophytes are concerned the economy effected in the single flower has rendered possible, in compensation, a larger annual output of reproductive units, but among these sciophytes reduction has led only to limitation of output and thus has the semblance of being imposed upon the organisms by unfavourable conditions.

In the list below generic names only are given. Apart from a few well-known plants the determination of the species of tropical forest plants leads by intricate paths beyond practical bounds.

MONOCOTYLEDONS.

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| Gramineae: <i>Panicum</i> , <i>Paspalum</i> , <i>Andropogon</i> , <i>Bambusa</i> . | Amaryllidaceae: <i>Fourcroya</i> , <i>Hypoxis</i> , <i>Curculigo</i> (escape). |
| Palmae: <i>Asterocaryum</i> , <i>Bactris</i> , <i>Calamus</i> , <i>Cocos</i> . | Dioscoreaceae: <i>Dioscorea</i> . |
| Araceae: <i>Anthurium</i> , <i>Philodendron</i> , <i>Dieffenbachia</i> , <i>Amorphophallus</i> . | Iridaceae: <i>Marica</i> . |
| Bromeliaceae: <i>Achmea</i> , <i>Tillandsia</i> , <i>Nidularium</i> , <i>Streptocalyx</i> . | Musaceae: <i>Musa</i> (escape), <i>Heliconia</i> . |
| Commelinaceae: <i>Commelina</i> , <i>Tradescantia</i> , <i>Dichorisandra</i> . | Zingiberaceae: <i>Hedychium</i> , <i>Costus</i> . |
| | Marantaceae: <i>Calathea</i> . |
| | Burmanniaceae: <i>Burmannia</i> . |
| | Orchidaceae: <i>Phyllurus</i> , <i>Ionopsis</i> , <i>Masdevallia</i> , <i>Cattleya</i> . |

DICOTYLEDONS.

- Piperaceae: *Piper*, *Peperomia*, *Artanthe*,
Ottonia.
 Moraceae: *Dorstenia*, *Artocarpus*, *Ficus*, *Cecropia*.
 Urticaceae: *Pilea*, *Boehmeria*, *Urostigma*.
 Loranthaceae: *Psittacanthus*.
 Balanophoraceae: *Lophophytum*.
 Aristolochiaceae: *Aristolochia*.
 Polygonaceae: *Coccoloba*.
 Nyctaginaceae: *Bougainvillea*, *Neea*.
 Menispermaceae: *Cissampelos*.
 Anonaceae: *Uvaria*, *Rollinia*.
 Lauraceae: *Ocotea*, *Nectandra*.
 Monimiaceae: *Siparuna*.
 Leguminosae: *Mimosa*, *Piptadenia*, *Desmodium*, *Enterolobium*, *Schizolobium*, *Bauhinia*, *Inga*, *Caesalpinia*, *Cassia*.
 Oxalidaceae: *Oxalis*, *Averrhoa*.
 Erythroxylaceae: *Erythroxylon*.
 Rutaceae: *Pilocarpus*, *Galipea*.
 Simarubaceae: *Simaba*, *Simaruba*.
 Meliaceae: *Cedrela*, *Carapa*, *Guarea*.
 Malpighiaceae: *Banisteria*.
 Vochysiaceae: *Vochysia*.
 Polygalaceae: *Polygala*.
 Euphorbiaceae: *Jatropha*, *Acalypha*.
 Anacardiaceae: *Anacardium*.
 Sapindaceae: *Sapindus*, *Paullinia*, *Cupania*,
Talisia, *Cardiospermum*.
 Bombacaceae: *Chorisia*, *Ceiba*.
 Sterculiaceae: *Sterculia*.
 Ochnaceae: *Gomphia*, *Luxemburgia*.
 Guttiferae: *Clusia*.
 Bixaceae: *Bixa*.
 Violaceae: *Anchietia*.
 Passifloraceae: *Passiflora*.
 Begoniaceae: *Begonia*.
 Lecythidaceae: *Lecythis*.
 Combretaceae: *Combretum*.
 Myrtaceae: *Psidium*, *Eugenia*, *Myrtus*.
 Melastomaceae: *Tibouchina*, *Melastoma*,
Miconia.
 Umbelliferae: *Hydrocotyle*.
 Sapotaceae: *Mimusops*.
 Ebenaceae: *Diospyros*.
 Apocynaceae: *Echites*.
 Asclepiadaceae: *Asclepias*.
 Convolvulaceae: *Operculina*.
 Verbenaceae: *Stachytarpheta* (colonist).
 Labiatae: *Leonitis*.
 Solanaceae: *Solanum*.
 Bignoniaceae: *Bignonia*, *Tecoma*, *Jacaranda*.
 Lentibulariaceae: *Utricularia*.
 Acanthaceae: *Justicia*, *Thunbergia* (colonist).
 Rubiaceae: *Psychotria*, *Mapouria*, *Amelia*,
Ladenbergia, *Uragoga*, *Palicourea*.
 Compositae: *Bidens*, *Stiffia*, *Mikania*.

CRYPTOGAMS.

- Filicales: *Aneimia*, *Trichomanes*, *Hymenophyllum*, *Lygodium*, *Davallia*, *Blechnum*,
Hemitelia, *Asplenium*, *Polypodium*,
Cheilanthes, *Doryopteris*, *Gymnogramme*.
 Lycopodiales: *Lycopodium*, *Selaginella*.

2. **Synecology of the Forest.** Rain forest is the climatic formation over almost all tropical South America, with the exceptions of the higher Andean region in the west, and the comparatively small portion of steppe called the "campos" in south-eastern Brazil. It is the largest area of jungle anywhere in the world. Thousands of square miles yet await exploration, in spite of all that has been done, and from the naturalist's viewpoint there are no limits to its possibilities.

It represents one formation, dependent on the climatic master factor (itself of course a complex of factors), over its whole area, but it presents a variety of associations determined by other circumstances, the effects of which cut across those of the climate, though about them we know extremely little.

Most writers tacitly regard montane and valley forests as representing different associations, and the palm-brakes of *Mauritia* and bamboos alongside rivers probably represent a third type, but that many more may exist, outside our knowledge, there is very little doubt. Diverse societies also occur, not directly dependent on environmental factors, but they are rare. Within each association-type the mixture is floristically very homogeneous.

These forests round Rio are practically all of the montane type. Valley forest is of a more advanced type, into which montane forest passes gradually with deepening of the soil and lessening of percolation. The chief area of valley forest is of course the Amazon basin. It is the ultimate climax association over the erosion level of all the rivers of that area.

The two types are often contiguous in occurrence, as for example in the Serra do Mar, within the present area. In this respect they are in a different category from the xerophytic forest which I propose to call "alpine forest," where direct continuity is only occasional and partial and depends on accidents of topography. Between the montane forest and the valley forest there is on the other hand a wide zone or gradient of transition, indicative in my belief of two associations that belong to the same formation. The valley forest differs floristically and in the more open texture of its undergrowth from the dwarfer but denser montane forest. The latter feature is traceable to the greater development of the high tree canopy, including certain enormous trees which protrude as conspicuous landmarks above the general level of the valley forests.

The view here expressed as to the status, in an ecological sense, of these forests is based upon that view which holds a formation to be a unit with a history, or in other words, a unit of vegetation which possesses a development in time, through all the diverse phases of which it is swayed by a limited and small number of supreme factors. These supreme or master factors may be temporary or quasi-permanent, but any change which occurs in a master factor brings to an end the succession which it governs and initiates a new formation. Each formation naturally tends in development towards a stable form of vegetation which will be coterminous with the master factors. The developmental period may be, and probably almost always is, short, relative to the endurance of the climax phase. The steps in development are to be regarded as our *associations* and, as they have no time dimension, but simply represent "types" of vegetation as we find them in any given place at any time, these associations are much more tangible than formations. Where the step from one phase to another involves a change in physiognomy, as for example bush-land to forest, it is clearly recognizable to all, but when the change is a slighter one, for example the replacement of certain species by allied or similar species, it may be liable to escape notice; yet such changes represent steps of development, just as truly as those in which the physio-

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gnomy alters. This is the case with the two associations here recognized. According to such views we may interpret these two associations, valley forest and montane forest. The latter is the earlier type, persisting on the higher ground, while the valley levels have developed a climax type of forest. On the hills a topographical factor, height, has cut across the master factor, climate, which is predominant, and has modified its potency so that two distinct types have come into being. As the valleys were formed the valley climate developed and with it the higher type of forest. As these mountains dwindle under the forces of erosion to the valley levels, the montane forest will pass over into the valley type, the change in time being similar to the change now observable in space. Taking the longest view, the one is a phase in the development of the other, and thus is amenable to the concept of an association. From the other point of view, we cannot, in the nature of things, possess decisive evidence as to whether a given association is the true climax of its formation or not. We cannot predict, we can so far only deduce. Granted this uncertainty however, there seems reasonable ground for believing that the forest of flat lands and valleys is a climax association, developed through dimly indicated stages from some plateau vegetation, and the forest of the hill slopes is a phase of its more immediate past.

Of the physiognomy of tropical rain forest much has been written, a lot of it considerably exaggerated, yet it is unquestionably one of the most impressive forms of vegetation in the world. From the exterior one notices that the upper surface, as it were, of the forest is more irregular than that of temperate woodlands. Not that the size of the trees is irregular, on the contrary especially big trees are rare and visible for a long distance as conspicuous landmarks, but the number of different kinds of trees is much greater than in our woods and a corresponding diversity of habit makes itself evident. Similarly the diverse tints of foliage and the sprinkling of vividly coloured flowers, both of the trees themselves and of epiphytes, decorate the forest in a way to which we are unaccustomed. In habit the candelabra-trees (*Garuga*, *Argyrodendron*, *Cecropia*, etc.) are the most noticeable irregularities, and in colour, *Cecropia adenopus* shows up a bright silvery grey, while *Melastomaceae*, *Bignoniaceae* and *Vochysiaceae* are constantly represented by masses of flowers among the tree tops. Indeed the richness of flowers on top is in striking contrast to the poverty below¹.

One or two features of the undergrowth of the trees strike the observer. One is the frequency of thorns on old stems, even, in fact, on the boles of big trees, such as the bombacaceous *Chorisia*, which render passage less pleasant than it might be. Another is the rarity of buttress roots in the American tropics, although winds of unsurpassed violence can occur here. Is this another "adaptation" which rests on deductive evidence only?

¹ The monograph by Wettstein (1904), in Karsten and Schenck's *Vegetationsbilder*, contains some fine illustrations of the forests of this area.

As we have remarked in the body of this article layering is distinctly traceable even amid the confusion of forms which fill the undergrowth.

The ground flora extends from 0-1 metre high.

The shrub flora from 2-5 metres high.

The tree flora from 10-25 metres high.

It is obvious that during the growth of a tree of the forest canopy it must pass through a deep biological change after growing up through the hygrophilous lower forest and emerging into the practically xerophytic conditions on top. Yet the later adoption of protective measures seems to be accomplished easily and, from what we have found regarding the atmospheric conditions in the upper layers of undergrowth, is probably brought about gradually. The lower branches of such trees are only sparsely developed and soon drop off, so that the tendency of the high trees is to form columnar unbranched trunks.

Compared with the bush layer the ground flora is comparatively open. Nearly all the species are perennial herbs, though prostrate creepers are not uncommon. They are plants of the deepest shade.

There is a natural interdependence between the extent of development of the three layers. Where the high forest is thinner the bush layer is correspondingly thicker and the ground flora lessened, and vice versâ. Where the shrub layer is decreased the ground flora is increased. The high forest and the ground flora go together in development. The shrub layer is opposed in development to both. Hence it arises that when a wood is partly cleared of trees for timber, the shrubs thicken to such an extent that an almost impenetrable bush is formed, while the ground flora suffers proportionately. Other factors, such as water, cause local increase in the ground flora, and Marantaceae form quite thick colonies in wet places. Palms themselves, chiefly *Bactris* and *Asterocaryum*, are not uncommon in the undergrowth, but where they form a dominant society they suppress almost everything else. This may be due to smothering by the large dropped leaves; otherwise it is not easily explained, for the light under the palms is, if anything, greater than elsewhere. The ground flora contains a large number of caespitose forms, which are well adapted for light reception, as the young leaves do not tend to shade the older ones. Fungi are extremely abundant on and in the forest floor, and to them probably is traceable the peculiar odour which permeates the forest everywhere, and is easily recognizable at home in the Kew hothouses.

Lastly there are the epiphytes. Their distribution in the forest is sporadic, and, so far as can be judged by observation alone, they favour only the lighter spots where partial clearing has occurred, and the margin of the forest. In the thinner parts of the forest, towards the upper margin on the hill slopes, they are much more abundant. Naturally this applies only to the Angiospermic epiphytes. Cryptogamic epiphytes flourish almost anywhere, Junger-

manniaceae and Lichens even high up on the tree trunks, and *Strigula* and its allies on the leaves.

Apart from regular epiphytes there is a large class of facultative epiphytes to which it is hard to set any bounds. Even large trees may grow upon others. The writer has seen such unlikely species as *Piptadenia communis* and *Cecropia palmata* growing as perfect epiphytes, and also, of course, *Ficus*, the classical example of this type. In these forests the myrmecophilous species *Cecropia palmata* and *C. adenopus* are common. It seems worth noticing that *C. palmata* was observed with its leaves dissected by the leaf cutting ants, although *Azteca* was living on it, and to all appearances quite active.

A "biological spectrum" of the forest flora, after the pattern suggested by Raunkiaer, would show an enormous preponderance of woody plants. This is the result of two interdependent factors, (a) the absence of any physiologically dry season and (b) the resulting continuous growth. The advantage conferred by mechanical strength, and the density of growth which results from this, have already been referred to. In spite of the diversity of species the appearance of the undergrowth is decidedly monotonous. There is an evident resemblance to the undergrowth of the evergreen Lusitanian and Mediterranean woodlands, allowing for differences of climate, especially in the prevalence of simple leaves of the *Laurus* type. Flowers are uncommon and inconspicuous except in the tree tops, where, even when they are individually small, they tend to form large inflorescences and show up as blazes of colour when forest clad slopes are seen from a distance. In my own small experimental area, a small patch of about a couple of acres was covered by a palm society, but otherwise the homogeneity of the floristic mixture was very marked all over. Similar "palm-pockets," which have also been noticed in the forests of the Philippines by Brown and Mathews¹, afford practically the only break in the general blend of species.

The appearance of homogeneity is greatly increased by the unity of type observable throughout, especially in leaf form, which must have been noticed by everyone who has occasion to deal with herbarium material. This seems to be the result of epharmonic convergence in Warming's sense. It is indicative of two things, (1) the antiquity of the prevailing conditions, which has allowed time for this convergence, and (2) the peculiarity of the conditions which has enforced it.

By peculiarity I mean divergence from the mean, and therefore difficulty for the organisms involved. That the conditions of life for the undergrowth are far removed from the mean is I think undeniable, but their difficulty has not been taken into serious consideration. The complexity of structure of the forest and the multiplicity of contained species have always been looked upon as evidence of extraordinary favourability. Now the complexity is largely a matter of density, and so dependent on the continuous growth

¹ *Philipp. Jour. Sci.* 9, Sect. A. See this JOURNAL, 3, 246.

period, while the multiplicity of species is better explained on the grounds of antiquity rather than of favourability, an idea which is seemingly erroneous. That there is a real difficulty involved is emphasized by the failure of the forest to regenerate quickly on *large* cleared areas, where the breakdown of the nutrition cycle has thrown conditions back practically to the starting point of the forest formation, but without the original soil to give the regeneration a start. Seedlings are plentiful within the forest, though I doubt if the trees of the highest forest regenerate freely, except in temporary clearings where some large individual has collapsed, but in a clearing of large extent things are very different.

The change brought about by clearance is probably largely due to the drying out of the humus colloids and the killing off of the micro-flora which linked together the two ends of the nutrition cycle by breaking up humigenous bodies and transferring the liberated food substances through the medium of mycorrhiza to the living host-plants.

That the forest as we find it now, only has a slight dependence on mineral soil nourishment is shown by the sterility of large cleared areas, except where the soil after clearing has been carefully treated and preserved from the evil effects of drying-out. On the other hand, small areas, sheltered by the surrounding jungle, reforest quickly.

Where the rainfall is exceptionally heavy, regeneration may be impeded by another factor, namely the bodily removal of the soil itself, or the entire nutritive contents of it, by the rain, when once the protective leafy covering is cleared off. The coarse grass land that takes possession of the cleared areas which have not been brought under immediate cultivation may in time regenerate humus and so permit reforestation, but the slowness of the process is evidence of the radical change brought about by clearance, and the considerable length of time that must have elapsed in the creation of the conditions prevailing in the fully developed rain-forest. The first development of the forest was no doubt accomplished under very much more favourable conditions than these, with a richer soil and fewer competing species. In those early phases or associations, when the forest type was first appearing, it may have been normally dependent upon the soil nutriment and nitrification as in temperate woods; but the present association is conceived of as a type which in the course of ages has, through the exhaustion of the soil, evolved a system of living largely upon the products of its own decay, i.e. upon salts and nitrogen liberated from humus through the agency of bacteria and fungi, and upon CO_2 liberated during fermentative decay. In a word, the life of rain forests hangs upon hyphae.

Montane forest in fact hardly depends upon the soil at all except for water and anchorage. Near Santos it is remarkable that the rain forest on small hills near the sea maintains its "complex" character right on to almost bare rock, where the general depth of soil cannot have been more than 3-6 ins., and that almost pure humus.

A curious phenomenon supports this theory of the rain forest, namely the possibility of its suicide, which could not happen were it not balanced as it is, plant against plant. A single constituent species forming, it may be, at first a small society in the forest, if favoured by local circumstances may spread to the eventual extermination of neighbouring species. If the unit be a high forest tree no serious change results, but if it be of another type, dependent on the existence of forest conditions, the ultimate result may be its own death also. A case of this latter sort has been observed by the author near the upper end of Rio Bay. The aggressive species was a *Calamus*, and the result was devastation of the forest. If the area involved be not large it will no doubt be rapidly recolonized; if it be large a change of formation might result. This must be a rare phenomenon but it is a real one.

Rain forest is presumably a climax association, but naturally only within the limits of its own formation, which is the climatic formation of the most of warm South America. It can be superseded, if another master factor supervenes over climate. Thus in the broad valley of the Rio Parahibuna, swamps are killing off the forest. The water-logging of the soil alters the master factor and begins a new formation.

NOTE. It is impossible to refer in detail to the very numerous points of contact between the present work and the extremely interesting investigations of Forrest Shreve (1914) on the Jamaican Rain Forests, to which general reference for a great deal of collateral information may here be made. His forests differ in many respects from mine, but the resemblances are more striking than the divergences. It is gratifying, therefore, to find that his main conclusions on the environmental conditions in rainforest harmonize satisfactorily with those now advanced for another geographical area.

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ON THE CAUSES OF FAILURE OF NATURAL REGENERATION IN BRITISH OAKWOODS.

BY A. S. WATT.

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INTRODUCTION. VIEWS OF PREVIOUS AUTHORS.

DESPITE the prolific production of ripe acorns in certain years, when the floor of our oakwoods is littered with fruits during the autumn, and when, during the following spring, millions of seedlings may be seen coming up through the surface layer of humus or among the herbaceous plants of the ground vegetation, yet the occurrence of natural regeneration of oakwoods in this country seems to be something of a rarity. If regeneration took the normal course, one would expect to find during the years subsequent to a "fall" a community of young oaks, some of which, sturdier than their fellows, would dominate and handicap the others in the struggle for existence, finally causing their suppression and death. The dominants, we should expect, would ultimately grow up to replace the aged stock. The following is an attempt to solve the problem and is a record of the causes responsible, so far as these have come under my observation or been ascertainable by experiment.

This enquiry is so intimately associated with the larger subject of the degeneration or retrogression of forests, that a brief review of the more important causes assigned may assist us towards a solution.

The reduction in the number of seed parents of both species of oak (*Quercus pedunculata* and *Q. sessiliflora*) due to the great demands upon oak for the Navy and to the encroachments made upon the forests by the peasantry for agricultural and pastoral purposes in former days not only reduced the area under forest, but deprived the woods themselves of the finest trees. Evidences of such are frequent in writings on Natural History or in works of general historical bearing or can be deduced from the Statutes passed from time to

time ordering the reservation of young oak¹. To repair this loss no adequate planting took place and the oak being a heavy seeded tree was slow in recolonising the land thus laid bare.

Krause² (1892) attributes the limiting of the forest area in North Germany to "errors in silviculture, especially to the grazing of cattle in the forest," and this may be legitimately applied to this country as cattle and pigs were formerly driven into the woods for pannage. This is generally conceded as a factor responsible.

Degeneration of woods due to the lack of suitable conditions for the germination of the seeds of the dominant species has been laid stress upon by Moss³. Similarly Henry⁴, quoting Schwappach in regard to continental soils, says, "Natural regeneration of the stock is rendered quite impossible on poor soils and more difficult on soils of better quality by the unfavourable modification of the surface covering (hardness, dryness) and by the stunting of the parents." Tansley⁵ also describes this in the case of the Damp Oakwood association of this country. "When the soil is left exposed to the sun and wind by excessive felling of standards or clearing of coppice, the humus layer is destroyed and the soil either becomes very weedy or cakes hard and becomes almost bare of vegetation. Under such conditions the natural regeneration of the wood from self-sown seed is checked or arrested and unless the wood is properly taken in hand it degenerates to scrub and grassland." Schlich⁶ and Forbes⁷ express similar views.

Degeneration has also been attributed to the impoverishment of the soil. A summary of Graebner's account of the degeneration of woodland in North Germany due to this cause is given in *The Woodlands of England*⁸, where we find that by the removal of tree trunks, by the leaching of the soil and by the spread of heath vegetation consequent on the formation of a moor pan, the ground is impoverished and the oaks die out without leaving successors.

Dealing more particularly with causes affecting the natural regeneration of oak, Forbes⁹ states that where acorns "were sown in small patches scarcely any (seedlings) made their appearance, though we could never discover what really became of them." Elwes and Henry¹⁰ and others testify to pigeons and pheasants devouring enormous quantities of acorns.

Regarding the influence of rabbits Percival Lewis¹¹ remarks of the New Forest about 100 years ago, "The rabbit in his pursuit of food did much injury and the cutting of browse wood as it was carried on in former times must have

¹ Cf. Nisbet, *Our Forests and Woodlands*, 1909, Chap. I, where quotations are given from Gilbert White's *Natural History of Selborne*, 1789, Holinshed's *Description of England*, 1577, *Statute of Henry VIII*, 1543, etc.

² Quoted by Moss, *Vegetation of the Peak District*, 1913.

³ Moss, *op. cit.*

⁴ Henry, *Les sols forestiers*, 1908.

⁵ Tansley, *Types of British Vegetation*, 1911.

⁶ Schlich, *Manual of Forestry*, Vol. II, 1907.

⁷ Forbes, *Eng. Arb. Soc. Trans.*, Vol. V, 1902.

⁸ Moss, Rankin and Tansley, *The Woodlands of England*, 1910.

⁹ Forbes, *op. cit.*

¹⁰ *Trees of Great Britain and Ireland*, Vol. II, 1907.

¹¹ Nisbet, *op. cit.* p. 102.

been attended with considerable depredations; the holly and the thorn are often the preservers of the seedling oak." Elwes and Henry also state that mice are the worst enemies of seedling oaks.

Upon the type of seed bed available for acorns Nisbet¹ remarks, "Owing to the want of close cover the soil often gets overgrown with grass or worse still with moss, and then a satisfactory crop of self-sown seedlings cannot be expected." Compare this with the observations of Forbes². "A grassy surface seems the natural seed bed of oak, for very successful examples may often be seen on rough pasture adjoining woods which for some reason or other has been allowed to lie waste or is only slightly stocked with cattle during the summer."

With regard to the supply of light necessary for oaks opinions vary slightly. Nisbet (*op. cit.*) says, "As soon as the seedling crop appears the seedbearers have soon to be removed because the young oak is impatient of even the comparatively light and broken shade cast on it by the parent trees." Warming³, however, remarks that "the common oak is a tree making moderate demands in regard to light."

The above are a few of the various causes assigned in the explanation of the failure of regeneration, and effects observed in particular instances may lead many foresters to attribute all failure to one or two particular causes. So far as I am aware no systematic attempt has been made to ascertain exactly how far each is operative and generally to find out as much as possible about the causes of the observed lack of regeneration.

The enquiry naturally falls into three sections, the first dealing with the fate of the acorn up to the time of germination, the second with the causes inducing the loss of germinative capacity, and the third with the establishment of the seedling and its subsequent history.

PART I.

ENEMIES OF THE ACORN UP TO THE TIME OF GERMINATION.

During the latter part of October, 1914, the floors of the various oakwoods in the vicinity of Cambridge were littered with millions of brown, well-ripened fruits. Visits during the next few weeks revealed a striking change in the number visible and one may account for this either by assuming that the acorns are removed or that they were now in some way concealed from view. Both these causes are in fact operative.

Dealing first with the latter it may be noted that the oak continues to shed its leaves long after the fall of the fruit—and this assists in the concealment of the acorns. Further if the wind has access to the floor of the wood, leaves may collect in certain sheltered spots, and in these the acorns are effectively concealed. Certain types of ground vegetation also are insufficiently closed to

¹ Nisbet, *op. cit.* p. 102. ² Forbes, *op. cit.* ³ Warming, *Oecology of Plants*, 1909.

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prevent the heavy acorn, in its fall, from at once reaching the soil surface, and in the case of a floor covered with humus the impact of the acorn is such as to form a sort of *nidus* which produces at least a partial embedding.

Nevertheless a careful note of the number of acorns on selected areas at successive dates established the fact that many were disappearing, and so complete was the removal in certain cases that by the spring of the following year great difficulty was experienced in finding even a few where thousands had fallen in the autumn. At the same time it was observed that where acorns had fallen among humus and become concealed through the subsequent fall of foliage, the rate at which they disappeared was decreased compared with the quick removal of those which had fallen on bare or comparatively bare areas.

Table I (plots 1-3) shows the rapid disappearance of acorns, when these lie exposed on the soil surface. Plots 4-7 (inclusive) indicate that a certain amount of protection is afforded by a humus covering as evidenced by the acorns' slightly longer survival. The value of protection against all but small animals is shown in plots 8-10 where the removal of all the acorns was somewhat delayed as compared with those completely exposed.

Table I.

No. of Plot	Type of soil covering	Oct. 22nd	Oct. 30th	Nov. 9th	Nov. 14th	Nov. 21st	Dec. 1st	Dec. 5th	Dec. 10th	Dec. 16th	Jan. 16th
1	On Humus ...		50	1	0						
2	On Moss ...		20	13	6	3	0				
3	Sparse covering of dry leaves ...				45	21	0				
4	Under 1 in. of humus ...	30	16	4	2	0					
5	"		25	0							
6	Under 2 ins. of humus		50	26	4	0					
7	"			25	25	24	13	0			
8	On Moss ...		30	13	6	3	0				
9	In Grass ...		25	17	16	11	1	1	1	0	
10	"			16	9	8	6		4		0

In the course of these observations evidences were not wanting of some of the agents responsible for the heavy mortality. Sometimes, where there had been once an abundance of acorns there remained later only pieces of broken pericarps. In others there was found among the humus a large number of acorns in all stages of mutilation, while the coincidence of the disappearance of a number of acorns planted below a humus covering 2 ins. in depth and the appearance of mice burrows in the area was suggestive. But a very large number of acorns must have been removed *in toto* as no traces of them had been left.

Foresters are generally agreed that rabbits eat large quantities of acorns, so plots temporarily protected against them were established. Nevertheless in due course all the acorns disappeared.

The foregoing observations suggested the following experiments which were carried out on light sandy soil in an open oakwood at Didlington near Brandon (Norfolk).

1. An area of about 144 sq. yds. was enclosed with wire netting of $1\frac{1}{4}$ in. mesh so as to exclude rabbits and mammals of similar size. The ground was prepared, about two bushels of acorns sown, and the whole then raked over so as to conceal the seed.

2. An area of about 16 sq. yds. was similarly surrounded and also covered over with netting to prevent attacks from birds, 50 acorns being sown on the surface and 50 planted below.

3. An area of 1 sq. yd. was enclosed by a wooden frame, the lower part of which was sunk 9 ins. into the ground. Over the top a double layer of netting of $\frac{1}{2}$ in. mesh was fixed. 50 acorns were sown on the surface and 50 below.

4. At the same time 30 acorns were planted below the surface unprotected in any way.

The results are set forth in Table II.

Table II.

No. of Plot	Number of acorns sown on 11th Dec.	18th Mar.	29th Mar.	30th June	8th Sept.
1	2 bushels				8 seedlings
2	50 on surface	0			
	50 below surface				35 seedlings
3	50 on surface	50	50	50	
	50 below surface	50	50	50	
4	30 below surface	30	1		

Near the above experiments the gamekeeper was in the habit of feeding the pheasants. From the testimony of both the gamekeeper and the forester of the estate, plot 1, with its newly turned loose sandy soil, was a great attraction for the birds, with the result as shown. Out of 2 bushels of acorns, only 8 seedlings appeared.

With regard to plot 2 all those acorns placed on the surface disappeared the following day, but of those below 35 germinated. Of the 30 planted under the surface without any protection only 1 remained. Nor does the pilfering cease after the seedling is established, as in an area protected from rabbits and birds 23 out of 24 had their acorns stolen.

The value of complete protection from animals is obvious from the results of plot 3 where all the acorns remained intact.

That burying in the soil by itself lessens the mortality is not apparent from the experiments. Where the soil is loose and easily turned over to be searched, the chances seem less favourable to survival than where they are embedded in hard soil. The success of regeneration after the pigs were driven into the forest for pannage in former days, may have been in part due to the concealment afforded by burial of the acorns. Also in woods where the work-

men in felling operations have trodden the acorns well into the soil regeneration at least in its initial stages has more chance of success. Mice cannot penetrate and search the surface 2 ins. of hard soil so completely as they would a layer of humus of equal thickness. In fact, the presence of the woodmen may have acted in two ways, by scaring the mice from the area of operations and by making the ground unsuitable for their occupancy for some time to come, thus diminishing the enemies of the acorns in the particular locality.

The foregoing experiments clearly demonstrate the value of protection against the attacks of animals. Exactly the share taken by the various agencies in the disappearance of the acorns in any given locality seems to depend a good deal on local circumstances, e.g. birds such as pheasants may be an important factor in one place and quite negligible in another. Further it is well known that rabbits tend to abound on light sandy soils so that they are ordinarily much more prevalent on soils such as bear the Dry Oakwood and Oak-birch-heath associations than on the clay of the Damp Oakwood. But mice seem more evenly distributed and are certainly a powerful factor militating against successful regeneration by their consumption of large quantities of the seed.

The following is a list of animals known to eat acorns¹:

Cattle, Red Deer, Fallow Deer, Roe Deer, Wild Pigs, Rabbits, Squirrels, Dormice, Forest Mice, Voles, Pheasants, Wood Pigeons, Jays, Rooks. The principal offenders are: Rabbits, Mice, Voles, Pheasants, Wood Pigeons, Jays.

PART II.

CONDITIONS AFFECTING THE POWER OF GERMINATION.

During the latter part of the year some acorns seem to escape the attention of those agents previously mentioned—acorns which look unhealthy, having lost their brown colour. Upon examination they are found to be the hosts of a weevil larva, which feeds on the kernel and ultimately destroys the acorn. Fabre² from observations on woods in France says, "More than the jay, more than the field-mouse, the elephant-beetle (*Balaninus elephas*) has contributed to reduce the superfluity of acorns." The beetle found in this country, viz. *Balaninus glandium*, is not so prevalent and the damage done is not extensive.

During the summer of 1915 in the course of visits to various oakwoods in the South of England, I found certain acorns which evidently had escaped the marauders, but which had not germinated. For the most part they lay

¹ Schlich, Nisbet, Elwes and Henry, *opp. cit.*

² *Social Life in the Insect World*, 1912.

among a litter of pieces of pericarps upon a soil surface, in places devoid of vegetation. The soil itself was light and sandy such as is characteristic of the Dry Oakwood or the Oak-birch-heath associations and characteristically flat and even, compared with that of the Damp Oakwood, where beneath the humus the soil is extremely uneven on a small scale, owing to the animals present in the soil piling it up in one place and leaving furrows or depressions in others. The surface was devoid of humus, except where the latter had collected in rabbit burrows, under the shelter of protecting brambles, in the lee of a fallen log, or in the sheltered parts of the wood. In areas such as these acorns were found lying, 10 months after their fall, still ungerminated. Nor do they after this lapse of time present the almost stony hardness or chocolate brown colour of the kernel such as is exhibited in most acorns exposed for a similar length of time in a room, the pericarp is whiter and the kernel seems quite fresh and capable of germination though somewhat shrunk, tougher and less brittle in texture than in a freshly ripened acorn. Such areas, devoid of humus and with sometimes a sparse vegetation of bracken or low growing mosses, were devoid of seedlings, in strong contrast to those places, perhaps a few feet distant, where the fallen leaves had collected. Considerations dealt with in Part I will partly explain the reason for this, but these do not explain why certain acorns overlooked by the despoilers did not germinate.

That such acorns did not represent the ungerminable portion of the crop, the following experiment will show. 25 acorns were placed on a surface devoid of vegetation and 25 below and the plot enclosed. Of the latter all germinated, but of the former none. The following experiments were undertaken to find out what essential factor was lacking from the germination requirements in the case of the acorns lying on the surface.

In these experiments carried out in a glasshouse where the temperature was that of an ordinary heated room, acorns obtained from Brandon were utilised. They were sent to me towards the end of October and, until I should require them for experiment, I kept them in a well-stoppered glass bottle. Of the exact interval which elapsed between the fall of the acorn until my receipt of them I have no precise information, but during that time there must have been a slight loss of moisture.

The experiments were divided into three sections, treating of:

A. The relation of the micropyle to water absorption.

B. The relation of the position of the micropyle to the soil surface and germination.

C. The relation of water supply to germination.

A. *Relation of micropyle to water absorption and loss.* The method employed to find out if there was any relation between the micropyle and water absorption or water retention was simply to seal up the micropyles of a number of acorns and to compare the loss or gain under different conditions with those unsealed.

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6 acorns, 3 sealed and 3 unsealed, were exposed to the atmosphere of the glasshouse for 34 days. The following were the results:

3 acorns unsealed and exposed had an average loss of 19·6 per cent. of the original weight.

3 acorns sealed and exposed had an average loss of 21·6 per cent. of the original weight.

At the same time 6 acorns, 3 unsealed and 3 sealed, were planted.







3 acorns unsealed and planted for 34 days gained 5·4 per cent. of the original weight.

3 acorns sealed and planted for 34 days gained 5·1 per cent. of the original weight.

From these results we find that by sealing the micropyle the retention of water is in no way assisted, whilst similar action does not impede the imbibition of water.

B. *Relation of position of micropyle to soil surface and germination.* Experiments were carried out with acorns which were partially buried in the soil to different depths, and whose long axes were placed at various angles to the horizontal. Table III shows the positions of the acorns, the shaded portion representing the amount buried, while the dividing line between the shaded and unshaded parts being horizontal *in situ*, shows the position of the acorn in the experiment.

Table III.

Position of acorn	Order of depth	Weight in grams		% Loss	Fate
		3.11.15	17.3.16		
	1 (deepest)	6·32	6·28	·60	Germ. $\frac{1}{4}$ in. then dried up
	2	6·97	6·94	·44	Germ. to seedling
	3	5·98	5·77	3·6	„ „ „
	4	7·28	6·67	8·2	No germination
	5	8·67	8·20	5·3	„ „
	6	6·77	5·82	14·0	„ „

Of the above 6, 3 germinated but only 2 developed to normal seedlings, the 3rd germinated $\frac{1}{4}$ inch then ceased to grow. It will also be seen that there

is a definite relation between germination and the percentage loss of water—the average per cent. loss of the 3 which germinated being 1.55, whilst the average loss of those which did not do so was 9.2 per cent. Further only those two whose micropyles were embedded in the soil developed to seedlings.

12 acorns were next inserted in the soil with varying amounts of each projecting, the first 6 having the micropyles pointing vertically downwards, the second 6 having these pointing vertically upwards. The results are given in Table IV.

Table IV.

	Height of part exposed	Weight in grams 2.11.15	Final weight in grams	Date of final weighing	% Loss or Gain	Fate		
Micropyle vertically downwards	12 mm.	6.15	6.01	9. 3.16	-2.3	All germinated to normal seedlings		
	" "	6.38	6.28	9. 3.16	-1.5	"	"	"
	11 "	5.52	5.65	21.12.15	+2.2	"	"	"
	6 "	7.70	7.78	21.12.15	+1.0	"	"	"
	5 "	6.96	7.07	25. 1.16	+1.56	"	"	"
	3-4 "	6.38	6.58	21.12.15	+3.0	"	"	"
Micropyle vert. cally upwards	15-20 mm.	8.67	8.22	9. 3.16	-5.2	No germination		
	17-18 "	8.94	8.60	3. 2.16	-3.8	Germ. $\frac{1}{4}$ in. then ceased		
	15 "	6.75	6.45	3. 2.16	-4.4	"	"	"
	10 "	6.17	6.29	25. 1.16	+1.9	Decayed		
	8 "	6.26	6.36	18. 2.16	+1.6	Germ. $\frac{1}{4}$ in.		
	Deepest	6.16	6.49	1.12.15	+5.3	Decayed		

Especially in the case of those acorns whose loss was small, the decrease was not continuous. Sometimes in the course of the weighings, the weight on a given date was greater than on the one preceding, owing no doubt to variations in the moisture of the air; and especially in the case of the last 6 there was difficulty in obtaining reliable data, as the basal ends soon began to decay. The general result, however, is clear that in the case of the first 6, planting with the micropyles downwards ensures success, while in the case of the second 6 even if a commencement of germination was made, this soon ceased. No doubt there was too much evaporation from the young radicle in the warm atmosphere of the room, and the supply of water not being rapid enough, it wilted and died. There would not, of course, be the same rapid evaporation in the open, where the temperature would be lower and the relative humidity higher.

C. Germination and the Moisture Supply. First an experiment was carried out to determine how much water an acorn can lose before its capacity to germinate disappears. According to Guppy¹ an acorn reaches a stable weight after it parts with 60 per cent. of its weight. After such a loss has taken place, however, many kernels assume a brown colour and a stony hardness and when supplied with all the requirements of germination fail to respond. Table V gives the amount of water lost up to date of planting and the acorns' subsequent fate.

¹ *Studies in Seeds and Fruits*, 1912.

Table V.

Weight on 2.11.15	Weight when planted	Date of planting	% Loss	Average %	Fate
5.59	5.24	23.11.15	6.3	7.3	Germ. and developed
7.82	7.27	"	7.0		"
7.73	7.06	"	8.6		"
5.66	5.16	15.12.15	8.8	11.8	Decayed
7.88	6.64	"	15.7		Germ. and developed
6.98	6.22	"	10.9		"
9.11	8.39	23.12.15	7.7	11.4	"
9.08	7.60	"	16.2		Decayed
7.16	6.42	"	10.4		Germ. and developed
6.83	5.41	1. 2.16	20.8	27	"
6.85	5.34	"	22.0		Decayed
7.83	5.49	"	29.8		"
9.94	6.73	"	32.3		"
6.61	4.59	"	30.6		"
7.27	5.78	"	20.4		"

Attention is here drawn to the individual differences among acorns in the amount of water they give up in a given time. We find that the average loss in weight of those acorns which failed to germinate even when a suitable environment was provided was 27 per cent. Taking the individual acorns it appears that 20 to 21 per cent. represents the critical loss of water, but this figure may be too low owing to the likelihood of a certain loss of water before my receipt of the acorns.

Again, 5 acorns were placed in a bottle containing some calcium chloride. After losing 26.8 per cent. of their weight they were planted and subsequently weighed one month afterwards. While these were in the soil they gained 30 per cent. in weight yet no germination ensued, the previous loss of water evidently destroying the viability of the seed.

Another experiment was started to find out whether acorns would germinate in an atmosphere of higher relative humidity, but with only a small part of their surface in contact with the soil. To this end depressions were made in the soil by packing the earth round a specimen tube 1 in. in diameter. Five such were made of varying depth and the acorns placed at the bottom, one to each depression. The following table gives the results.

Table VI.

Depth of depression in mm.	Weight on 1.11.15	Weight on 16.3.16	% Loss	Fate
35	6.23	5.98	4.1	No germination
25-30	6.01	5.75	4.2	"
20	6.84	5.38	21.3	"
18	6.99	6.57	6.0	"
15	7.89	6.85	13.2	"

So that in spite of the diminished loss of moisture no germination ensued.

A comparison of the loss of water in the preceding experiment with the loss from acorns lying on the surface of the soil, and acorns lying on paper entirely exposed to the atmosphere of the glasshouse is instructive.

Average loss of water from acorns in depressions during 19 weeks = 9.7 per cent.

Average loss of water from acorns on soil surface during 19 weeks = 22.5 per cent.

Average loss of water from acorns on paper during 19 weeks = 36.5 per cent. This at least shows the value of even contact with the soil in lowering the net loss, while an atmosphere of greater relative humidity assists still more in that direction. In no case, however, did germination occur.

We have seen that after the acorn has lost a certain percentage of its water even if it be thereafter placed under suitable conditions for germination there is no response beyond the merely mechanical imbibition of water. Further that even if the amount of water lost is much reduced by simply placing the acorns on a soil surface or still more so by placing them in depressions in the soil there was no attempt at germination on their part.

In these experiments we are dealing with acorns which have in part at least entered the resting stage so that there can be no question of vivipary as is noted by Guppy¹. While therefore the acorns in the above experiments which lost on the average less than 27 per cent. of water germinated normally when planted, those which lost a very much smaller amount, but placed under different circumstances as regards water supply, did not do so, and there seems ground for believing that conditions suitable to the germination were not provided in the latter case. Again the above-mentioned author gives the case where acorns germinated whilst actually drying but adds, "that in most cases the loss of water is too rapid and the tendency to proceed at once to germinate is suppressed." In the above experiments the temperature was the same in all, the supply of oxygen was sufficient, so that *ceteris paribus*, one is led to the conclusion that the inhibiting factor has some relation to the supply of water.

Under the soil surface the seeds are in direct contact with a film of water, and under these circumstances they absorb water mechanically. Now in the case of an acorn lying on the soil surface, either in a depression or on level ground, there is only a small part of its surface actually in contact with a film of water, the remainder being surrounded by an atmosphere with a relative humidity varying according to circumstances. The problem resolves itself, therefore, into an investigation as to whether acorns can utilise this atmospheric moisture for germination. In the experiment with the acorns in depressions one of the acorns gained 1.9 per cent. in weight, a percentage which closely approximates the hygroscopic figure given by Guppy, viz. 2-3 per cent. about a mean.

¹ Guppy, *op. cit.*

A brief consideration of the occurrence of vivipary in acorns as dealt with by this author will assist us to understand the results of the experiments given later. He clearly shows that acorns freshly detached hold more water than is actually required for their germination and can proceed at once to germinate without any external supply. "In fact we have seen that such acorns will germinate without a rest period after losing a good proportion of their weight by drying. Any check to the drying process of the fresh detached nut would directly aid the seed in proceeding continuously with its growth and dispensing with the usual period of repose." Further, "we may infer from Berthelot's principle that hygroscopicity being associated with the water which the seed, living or dead, holds in maintaining its equilibrium with the air, has nothing to do with germination," and thereafter he states that the germination observed where the atmospheric moisture was apparently utilised was in reality due to the fact that the acorn used its own excess water for this purpose. In this case the acorns were kept in the atmosphere of an unheated room in Devonshire, where the conditions are very humid and may have imposed a check on the drying process. The percentage germination under these circumstances was in one case 20, and in the other 23, so that $\frac{1}{2}$ to $\frac{1}{4}$ of the acorns concerned were able to utilise this excess water—an excess which he estimated at about 10 per cent. of the original weight of the acorn.

Owing to my inability to procure fresh acorns of either *Quercus pedunculata* or *Q. sessiliflora*, acorns of *Q. Cerris* were utilised in the following experiments in an endeavour to show that after a percentage of water is lost, acorns cannot absorb sufficient from the atmosphere to enable them to germinate.

Table VII shows the results of suspending over water, in a corked bottle, freshly collected acorns.

Table VII.

Original weight	Weight after one week	% Loss	Fate
2.812	2.728	2.9	Germinated
2.215	2.106	4.9	"
2.857	2.751	3.7	"

The acorns were presumably utilising their excess water for germination—a process which continued in spite of the loss of moisture.

Table VIII.

	Original weight	Weight before suspension or planting	% Loss	Greatest weight during next 6 weeks	% Gain	Fate
Suspended	3.112	2.820	9.3	2.897	2.7	No germination
	2.592	2.350	9.3	2.375	1.6	"
	1.727	1.550	10.2	1.606	3.6	"
Planted	3.652	3.194	12.5	3.580	12.8	Germinated
	2.392	2.158	9.7	2.415	11.9	"
	3.215	2.800	12.9	3.246	15.9	"

In the next experiment (Table VIII) 6 acorns were exposed in a room until about 10 per cent. of their original weight was lost. 3 of these were then suspended over water and 3 planted.

These results show that while the planted acorns absorbed the quantity of water lost and proceeded to germinate, those suspended in an atmosphere saturated with water vapour absorbed a small percentage only while no germination ensued.

From a consideration of Guppy's experiments and of those described above, one is led to the conclusion that an acorn has two chances of germinating, either, if conditions are suitable, proceeding with germination straight away before it has lost 10 per cent. of its weight (Guppy's estimate), or if the amount lost exceeds 10 per cent. but does not exceed 27 per cent.¹ that germination will take place only if the acorns come in contact with a film of water such as is provided for them in the soil. If the latter is not provided and the seed can absorb from the atmosphere only the water of hygroscopicity, then germination will fail.

A comparison of the method of storing acorns for spring sowing in this country with that in vogue on the continent, will show to what practical application the above information may be put. Among some foresters and seedsmen in this country the method employed is simply to collect the acorns in sacks and leave them there until required. Energy is set free in respiration and the acorns "heat." A large proportion make use of their excess water and proceed to germinate, with the result that the percentage germination in spring is very low. On the continent much greater care is taken. The authors of the *Neudammer Förster Lehrbuch*² give the following directions. "If the acorns....are to be kept until next spring, they must first dry. To that end they are piled up on a floor, about 20 cms. high, and turned over once or twice daily, until they are no longer moist externally. Nevertheless the drying must not go so far that the kernel becomes loosened from the pericarp, and the latter becomes wrinkled. Further storage results best in a (specially constructed) shed, less well on house floors in 30 cms. deep layers, mingled with dry sand. The fruits are turned over perhaps every three weeks, and also as soon as they show signs of 'heating'; thus especially at the beginning of and during unusually damp weather, caution is recommended." Here we have the precaution taken first to initiate the drying process to prevent the acorn utilising its excess water, and secondly to ensure that this drying process does not go beyond the "death point" of the acorn.

This check to the drying process mentioned above is brought about in nature by the provision of a seed bed which has an atmosphere more or less saturated with water vapour. Conditions vary in different woods and in different parts of the same wood and those necessary for successful germination may be brought about in a variety of ways.

Whether in the Damp Oakwood, Dry Oakwood or Oak-birch-heath as-

¹ Or perhaps 21 per cent., see p. 182.

² 1902, p. 148.

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sociations, wherever there is a covering of humus over the acorns, there germination is successful. In depressions in the soil where a few leaves can collect and form humus, there are often found many seedlings, e.g. in the entrances to disused rabbit burrows. Further in the lee of fallen branches or where the leaves have been caught, when urged by the wind, among the stems and branches of low growing shrubs such as Hawthorn (*Crataegus monogyna*), Blackthorn (*Prunus spinosa*), and Brambles (*Rubus* spp.), among the stems and fronds of bracken (*Pteris aquilina*) or among *Vaccinium Myrtillus* and *Calluna vulgaris*, there do we find numerous seedlings coming up. Again among grass such as meadow grass, acorns germinate in great numbers—a fact noted by Forbes¹ and also by Warming² who says, "If we were to leave these (meadows and pastures) to themselves, in time they would certainly give way to forest." A carpet of *Sphagnum* spp., or *Polytrichum commune*, provides also locally a suitable seed bed for germination, as I have observed in the New Forest and elsewhere.

The above data appear quite sufficient to show that in all the cases cited, conditions are such that the necessary environment is provided to inhibit the drying process, to allow the acorn to proceed at once with germination or prevent the removal of too much moisture before it can do so. During the autumn in such situations thousands of acorns are in fact found germinating.

Regeneration is often successful after felling has taken place; for this reason probably, among others, that the acorn becomes embedded in the soil and even if it has lost a certain percentage of water it can absorb sufficient for germination. In the old days, also, when pigs were driven into the woods for pannage those acorns which escaped their voracious appetites were either trodden into the soil or buried by the upturned turf, thus concealing them and providing a suitable seed bed³.

Let us review briefly the situations upon which acorns were found ungerminated. They were found upon soils characteristically flat, almost devoid of vegetation, without humus and of a light sandy nature. The evaporation from such a bare surface is much greater than from a surface where leaf mould is present. The following figures are taken from Schlich⁴ quoting Ebermayer.

Evaporation of water from soil in the open placed at 100 parts.

„ from forest soil without leaf mould = 47 parts.

„ „ „ with a full layer of leaf mould = 22 parts.

So that from a bare surface the evaporation was more than twice as much as from a soil covered with leaf mould. Should acorns fall on such a surface their drying process would immediately commence and their germination would be inhibited. These acorns, once they have lost a certain proportion of their moisture, cannot then absorb sufficient from the atmosphere to induce ger-

¹ See p. 175.

² *Oecology of Plants*, p. 323, 1909.

³ Nisbet, *British Forest Trees*, p. 207, 1893.

⁴ Schlich, *Manual of Forestry*, Vol. I. p. 40, 3rd Ed. 1906.

mination and unless they come in direct contact with a film of water which can be imbibed mechanically, there is no hope of their germination.

Whilst I have not found upon bare areas on a clay soil any acorns lying ungerminated during the summer, where the general evenness of the surface and lack of vegetative covering, either living or dead, identify it with the above, I have found small seedlings 1-1½ ins. high projecting from small cracks in the soil and upon closer examination it was found that the acorns which had lodged there had been afforded concealment and conditions suitable for germination. It is not that the soil is too hard for the penetration of the radicle, requiring to be "wounded" on this account, but that under these circumstances the acorn does not find a suitable haven where its moisture can be conserved, and tilling of the soil and covering of the seed are necessary either to provide this or supply the acorn with the necessary water if it has parted with too much. Not that "screefing" or "wounding" is not a desideratum for the better growth of the seedling but it is unnecessary to ensure physical ability of the radicle to penetrate the soil.

A similar result to that occurring on bare soil may be caused by a rank growth of herbage, which may prevent the acorns from reaching the soil and expose them to desiccation. "All foresters are agreed that in felled areas, invaded by a thick carpet of tall grasses such as *Molinia caerulea*, *Poa nemoralis*, *Poa sudetica*, various *Festucas*, etc., regeneration does not take place and one is obliged to break this carpet by 'screefing' so that the seed can fall on the damp soil, there to germinate and take root. Otherwise the seeds suspended on the vegetation are desiccated and lose their germinative capacity¹."

Again where such species as *Deschampsia flexuosa* and *Festuca ovina* form a mat on the soil surface, acorns readily lose moisture, the brown colour of the pericarp becoming white. Although on such situations I have found no seedlings, the cause may readily be assigned to those factors mentioned in Part I, but the change of colour of the pericarp has been noted before the acorn's disappearance. On this subject Moss² writes, "A matter which is not sufficiently emphasised is that in a closed plant association seedlings especially of plants with large seeds like the oak are rarely found. Now as time goes on the ground vegetation of a wood tends to become closed; and this simple fact in itself is one of great importance in the question of the rejuvenation or degeneration of forests. Some foresters make use of their knowledge of the fact and go to great trouble in keeping the ground vegetation open by removing the woodland weeds."

With regard to the effects of a grassy covering of the soil, however, there does not seem to be a consensus of opinion. For the natural regeneration of the oak under proper silvicultural methods, preparation of the ground is advocated³. In a contribution to the Société Centrale Forestière de Belgique⁴

¹ E. Henry, *op. cit.*

³ Cf. Schlich, Nisbet, Forbes, *op. cit.*

² Moss, *op. cit.*

⁴ Soc. For. de Belgique, 1909, p. 633.

entitled "La Forêt de St Michel," the author says, "Do we not often exaggerate the difficulty and the uncertainty which the sowing of acorns, whether natural or artificial, presents? I confess for my part, to have seen this carried out with complete success in Prussia under conditions which formerly had appeared to me purely utopian. Among the undergrowth (prés-bois) of the forest of Bramvald, the oak regenerates itself to perfection on a soil, superficial, degraded, and covered with thick grass. There is produced by natural and artificial sowing in the forestry canton of Salmünster (Spessart) admirable stocks of oak on soils invaded by *Calluna* and *Vaccinium*. Far from condemning these two plants, which, however, receive scant consideration in the forestry world, the forester of Bramvald looks upon their presence, but not their superabundance (that goes without saying) among the trees to be regenerated with satisfaction. If they are harmful inasmuch as they produce acidic humus, they conceal the acorns and young plants from forest animals especially from game."

These two expressions, seemingly contradictory, may be harmonised if we consider the type of ground flora more in detail. Undoubtedly where the acorns fail to reach the ground and are desiccated, or even if they germinate and the radicle fails to find a suitable medium before that occurs, regeneration will not take place. Or even if they do reach the soil and germinate normally but the seedlings are quickly overtaken by tall herbaceous species the chances are very much against their establishment. Now in pastures where grazing occurs and the acorns lie on the soil, germination is good and the establishment of the seedling seems assured if such grazing ceases and the seedlings grow up amidst grass which is not tall enough to cut off the supply of light. The determining factor seems to be whether the ground association is absolutely closed throughout the year, preventing the germination and establishment of the seedling, or, if not closed, the constituent species of this association forming a rank growth sufficient to cut off the light supply if germination takes place. From an examination of the list of species (v. *Types of British Vegetation*, p. 81) to be found in the ground flora of a Damp Oakwood, and from my own observations on a wood of this type, the herbage does not form an association close enough nor of such rank growth as to prevent the germination and establishment of the seedling. Undoubtedly from a strictly silvicultural point of view the removal of any rank growth is a desideratum, but where there is a plentiful crop of acorns, regeneration need not cease to take place solely on account of the presence of such. Such regeneration may be patchy but there would certainly be enough seedlings to ensure the continuance of the forest, or in other words to ensure successful natural rejuvenation.

Further, there seems to be no inherent difficulty in the recolonisation of scrub or neutral grassland by the oak, if other factors such as the grazing of animals were eliminated. In this connection the reader should compare Warming's remarks, previously quoted, on the invasion of pastures and meadows.

A study of the plant formation of the older siliceous soils, while presenting a ground flora in the damper parts of the oakwood association similar to that of the Damp Oakwood of clays and loams, and consequently not unsuitable to the germination of acorns, does not indicate the same suitability as a seed bed for these in the scrub and grassland associations to which the highwood may degenerate. From a comparison of the lists of species characterising the ground flora of the woods of *Quercus sessiliflora* and of the associated scrub (for lists see Moss, *op. cit.*) we find that in the latter, plants of the wiry type, e.g. *Deschampsia flexuosa*, *Festuca ovina*, etc. predominate, tending to form a mat on the ground surface. Acorns falling upon such springy turf would tend to bounce upwards and then lie loosely on the surface. Were such grasses to form a closed association, and in consequence be the only seed bed available for acorns from the occasional oaks, the conditions are such as to expose the acorns to the desiccating action of the wind, and as we have seen they cannot regain sufficient moisture from the atmosphere. This may be a partial explanation at least of the lowering of the altitudinal limit of oak on the Pennines. Other factors such as the "indiscriminate felling of trees and the grazing of quadrupeds" may in part initiate such a degeneration from the typical oakwoods to scrub, but once the ground association becomes closed by such grasses as the above it is difficult to see how regeneration can take place. The initiation of this process of retrogression may also take place in those drier parts of the wood where acidic humus is present in good quantity—a surface layer which is very favourable to colonisation by *Deschampsia flexuosa* (noted by Moss and Woodhead) whose "dense dry wiry tussocks" would present an unfavourable medium for the germination of acorns. The difference in the water content of the soil, correlated with the formation of acidic humus, by favouring the growth of these grasses, prevents successful regeneration of the oak.

The Dry Oakwood association presents a rather varied ground flora according to the character of the soil and the supply of light which reaches the ground. The soil of this association is characteristically poorer in humus than that of the Damp Oakwood but wherever we find the leaves collecting, there do we find germination normal. Also in those parts of such woods where the ground flora consists of herbaceous species which do not form a springy turf, and which do not impede the acorn in its fall from reaching the soil, seedlings appear in normal numbers. Similarly a *Holcus mollis* society, the intervals between the constituent members of which are occupied by humus, furnishes seed beds favourable to the germination of acorns, as I have observed in oakwoods in Suffolk. Parts of such woods are, however, often occupied by *Deschampsia flexuosa* and where this forms a close mat, the conditions are similar to those previously mentioned in the case of scrub on the Pennines. Bracken is also locally abundant in such woods, but its influence will be discussed later.

After explaining Graebner's account of the degeneration of oak forest to

heath by impoverishment of the soil, the authors of *The Woodlands of England*¹ go on to say that the replacement is much accelerated by the felling of trees. "This tends to rapid deterioration of the soil through destruction of the mild humus by sun and wind, and on suitable soils enables certain mosses and other plants of the heath association to find an entry. Not only does the felling of mature trees considerably diminish the supply of seed, but there can be no doubt that the occupation of the soil by a heath vegetation with its accompanying layer of acid peat, checks or altogether arrests its recolonisation by such a tree as the oak. This is perhaps due to unfavourable conditions of germination." On account of the open character of the wood, far more light is allowed to reach the ground and where exposed to the action of the wind the ground is swept clear of all the fallen leaves. Conditions are suitable for the propagation of *Deschampsia flexuosa* which is the characteristic grass of the Oak-birch-heath association, and where bare areas occur, or areas with only sparse bracken, as under isolated oak trees, the conditions for germination prove unsuitable and regeneration becomes impossible. Where *Vaccinium Myrtillus* or *Calluna vulgaris* has stayed the flight of the leaves, acorns, if they fall among these, germinate quite normally.

A general review of these associations of oakwoods leads one to the belief that areas unsuitable for acorn germination become increasingly frequent as we pass from the Damp Oakwood to the Oak-birch-heath, and even supposing the acorns to be left intact we should expect seedlings to diminish numerically as we pass from the one association to the other, not only because of the decreased number of parent trees, but also on account of the considerations mentioned above.

PART III.

ESTABLISHMENT AND FATE OF THE SEEDLING.

In spite of the vast mortality among acorns and the failure to germinate on certain areas, we find in certain places during the following spring thousands of seedlings pushing their way through the humus or soil. Yet, in 3 or 4 years' time, or less, nearly every one of this large number has disappeared. We have now to deal with the causes of this disappearance.

To find out whether the type of soil inhibits germination in any way 100 acorns (50 *Q. pedunculata* and 50 *Q. sessiliflora*) were planted in each of the following three kinds of soil, viz. loam, chalk, and acid peat bearing *Calluna*. The germination varied between 96 per cent. and 100 per cent. and was therefore normal in all cases.

Another experiment was carried out to ascertain whether depth of planting in humus had any inhibitory effect. A control plot where ordinary garden soil was used was also planted. 15 acorns were planted at successive depths of 3, 6, and 9 ins. in each. The results are given in Table IX.

¹ Moss, Rankin and Tansley, *The Woodlands of England*, 1910.

Table IX.

	In Humus			In Soil		
	ins.	ins.	ins.	ins.	ins.	ins.
Depth of planting ...	3	6	9	3	6	9
No. planted ...	15	15	15	15	15	15
No. germinated ...	11	9	12	8	10	10

The poor germination may be accounted for by the fact that out of every 15 in each layer, 10 were from acorns kept in a room for some time and the remaining 5 were collected in woods in the neighbourhood of Cambridge, where by that time (March) they were extremely difficult to get, so effectively had the agents mentioned in Part I diminished the supply. Nevertheless so far as the experiment goes it shows that planting in humus to a depth of 9 ins. did not interfere with germination.

The conditions under which acorns may proceed to germinate are described in Part II and even on bare soil the acorn, by utilising its excess supply of water, may germinate, especially if the surroundings are humid enough to impose a check on the drying process, as e.g. in a society of *Mercurialis perennis*, which Salisbury¹ has shown occupies the damper soils. Among grass many germinate and establish themselves, but on bare soil, while some may do so, a certain percentage, depending on the conditions, die either from the effects of frost or simply from desiccation through the exposure of their radicles.

Given that the seedlings establish themselves we have still to account for their disappearance later. With a view to identifying the causes of disappearance, I marked in 1915 certain areas in woods at Midhurst in Sussex and in Staffhurst Wood, Surrey (on the Kentish border) and visited them periodically. Certain areas were chosen where rabbits were known to be absent, others quite exposed to animals were marked and a few were enclosed. By utilising a method similar to that adopted to establish the fact of the disappearance of the acorns (Part I) the same was ascertained to be true of the seedlings.

The following results (Table X), compiled from a selection of a number of plots, give the fate of the seedlings up to January, 1916, i.e. 8 months or less after their germination. The third column gives the number of seedlings at the commencement of observations, the last the number in Jan. 1919.

In the following compilations it is necessary to point out that difficulty was experienced in relegating certain of the seedlings to their respective groups, e.g. the amount of shoot absent distinguishes the "cut off" from those with "tips off," and clearly such a division is an arbitrary one. Further difficulty was experienced in distinguishing certain seedlings, whose tips had withered through the agency of a fungus and subsequently fallen off, from those with their tips off through the action of herbivorous animals, the uppermost part

¹ "The Oak-Hornbeam Woods of Hertfordshire." *Journ. of Ecology*, 6, p. 33, 1918.

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Table X.

On sandy soil, exposed and left to natural agencies.

No. of Plot	Description of plot	Initial No. 1915	No. in January, 1916					No. in Jan. 1919
			Normal	Dead	Diseased	Cut off	Tips off	Missing
1	1 in. humus. No vegetation, dense shade	39	5	14	5	7	6	2
2	Under dense shade of Rhododendron	18	2	3	5	8		0
3	1 in. humus among some brambles	255	31		2		50	172
4	Open association of grass with thin carpet of leaves	17	6		10			1
5	1 in. humus. Light canopy. Bracken present but fronds removed	250	32		6	87		125
6	Among brambles, soil with some leaves but mostly bare	17	5			1	4	7
7	Deep humus. Light canopy. No vegetation	23	5		1	12		5
8	Among humus. No vegetation	25	7	1	3	1	10	3
9	Bare soil, afterwards shaded by bracken	17	1			3		13
Totals ...		661	94	18	32	119	70	328
% Totals ...			14.2	2.7	4.8	18	10.6	49.6

less than 1

Table XI.

On sandy soil, enclosed against rabbits or where rabbits were known to be practically absent.

No. of Plot	Description of plot	Initial No. 1915	No. in January, 1916					No. in Jan. 1919
			Normal	Dead	Diseased	Cut off	Tips off	Missing
1	In deep humus. No vegetation	91	65	6	16		1	3
2	Area in part bare, exposed to full sunlight	12	10				2	5 (av.)
3	Among grass. Light canopy	127	84	1	7	13	16	6
4	1 in. humus. No vegetation	57	5		1	27	4	20
5	" " "	24				17		7
Totals ...		311	164	7	24	57	23	36
% Totals ...			52.7	2.2	7.7	18.3	7.4	11.5

6.4

Table XII.

On sandy soil, enclosed from all animals.

No. of Plot	Description of plot	Initial No. 1915	No. in January, 1916						No. in Jan. 1919
			Normal	Dead	Diseased	Cut off	Tips off	Missing	
1	Area mostly bare. In full sunlight	130	126	1				3	116
2	1 in. humus. Bracken present but removed	17	16	1					14
3	2 in. humus. Dense shade. No vegetation	333	65	21	243	3?	1		0
Totals		480	207	23	243	3?	1	3	130
% Totals			43.1	4.8	50.6	6?	.2	.6	27

Table XIII.

On clay, unenclosed.

No. of Plot	Description of plot	Initial No. 1915	No. in January, 1916					No. in Jan. 1919	
			Normal	Dead	Diseased	Cut off	Tips off		
1	1 in. humus. Under shade, no vegetation	36	14		1	14	4	3	2
2	1 in. humus. Open ground floor	95	62	4		14		15	3
3	" "	7	7						0
4	Beech and Oak canopy. Open <i>Scilla nivalis</i>	26	13	3		2		8	0
5	Open association of vernal species	36	9	4	2	8	3	10	0
6	Open canopy. Varied ground flora	48	44	2		2			16
Totals ...		248	149	13	3	40	7	36	21
% Totals ...			60.1	5.2	1.2	16.1	2.8	14.5	8.5

of the remaining shoot then withering up and presenting a similar appearance. Also, during the course of early summer young seedlings appeared in certain plots, thus creating a difficulty in separating those previously observed from those coming up later. Where this occurred a conservative attitude was adopted and the data on that account may not represent the full ravages of the marauders. Further I have included in the column of "normals" those plants, which while the leaves were attacked by a fungus, yet had not then reached the dying or badly diseased condition, for as will be explained later most of the seedlings observed showed the presence of a fungus. On account of the above and of certain minor difficulties the percentages may be elastic to the extent of 2 or 3 per cent.; but this does not affect the main result.

The Effect of Animals.

Omitting those which are classed as "missing" and grouping those which are "normal," "dead" and "diseased," and comparing the results with the combined "cut offs" and "tips off," under varying exposure to animals, we arrive at the following percentage results (Table XIV, compiled from Tables X, XI and XII only) of seedlings surviving in January, 1916.

Table XIV.

		Exposed to animals	Protected from rabbits	Completely protected
Normal	14.2	52.7	43.1
Dead	2.7	2.2	4.8
Diseased	4.8	7.7	50.6
Totals	21.7	62.6	98.5
Cut off	18	18.3	.6?
Tips off	10.6	7.4	.2
Totals	28.6	25.7	.8

These figures are very significant, as showing in the first place the relative percentages which remain in the exposed, partially protected and completely protected plots, 22, 63 and 98.5, respectively. Secondly there is a decreasing percentage of those whose shoots are cut over as we pass from the exposed to the fully protected.

If we examine the columns of those "missing" we find a similar diminution as we pass from one series to the other, there being 49.6 per cent. classed as such in the exposed, 11.5 per cent. in the partially protected and less than 1 per cent. in the fully protected—a decrease which suggests a certain relationship between protection and those agents which such protection excludes.

In this way we get a series of figures which definitely show the value of protection against those agents which are responsible for the disappearance or for the cutting over of the seedlings.

During the course of these observations I repeatedly found seedlings which had been cut off about $\frac{1}{2}$ –1 in. above the surface of the ground, leaving a short stump, and the remainder of the aerial part either removed or lying near. Further in humus I often came across seedlings remaining in the upright position, with the leaves wilted and dry but still attached. Upon my pulling the seedling, I found it to come away quite easily and upon further examination discovered that it had been cut through below the surface level of the humus. Such areas were also undermined with numerous tunnels of small burrowing animals. The supposition naturally suggested itself to me that in the latter case at least, voles and mice in the course of their burrowing through humus found a shoot or radicle of a seedling in their way and simply gnawed it through. Such an explanation, however, did not account for those seedlings which had been cut over above the ground surface. I therefore watched a particular plot,

and after I had waited a short time a mouse made its appearance from a burrow in the area marked, and after a preliminary circumspection went to a seedling and gnawed through the shoot. It then proceeded to another and did the same again, the shoot toppling over and lying on the soil. No attempt was made in this case to look for the seedlings' acorns. I presume the explanation is that mice, being rodents, require some suitable material to gnaw in order to wear down their continuously growing incisors and evidently the shoot of the seedling oak is to their liking from this point of view.

As a result of these observations I made a separate column in the above data for those "cut off."

It is the unanimous testimony of foresters, whether expressed orally or in the literature of forestry, and also of workers in ecology, that rabbits do extensive damage in woods, and by eating the seedlings impede or wholly prevent natural regeneration. I have never actually seen rabbits thus engaged, but the opinion is so unanimous and so well established that we may assume they eat oak seedlings. Now the damage done to seedlings may be exactly identical with that done by mice except that in the former case no shoot remained by the side of the stump (although this is by no means invariable in the case of mice) the leaves and shoot evidently providing the rabbit with provender. The more woody parts of the seedlings are, however, seemingly unsuitable, as on several plots many bits of shoots were found. In other cases only the leaves and tips of the shoots were taken, and in still others only the leaves, short parts of the petiole with sometimes parts of the blade remaining attached—a distinction which is of value in distinguishing the stripping of the shoots through the agency of rabbits from stripping due to the fall of the leaves after their death has been brought about by disease. In many cases after this cutting off or stripping occurred, latent buds produced new shoots, which in turn were cut over and in some cases even a third shoot was put forth. Against such attacks the seedlings cannot hold out indefinitely.

The relation between the number reported missing and the degree of protection afforded has already been noted. If we discount the percentage missing in the enclosed areas (a percentage less than one) and deduct those missing through other agencies than rabbits from the percentage thus reported in exposed areas we get $(49.6 - 11.5)$ 38.1 per cent. still unaccounted for. The explanation of this may be that not only do rabbits nibble seedlings but may gnaw them off so close to the ground that on subsequent visits there were no subaerial parts left on which to base observations.

The actual damage done by rabbits varies of course in different places according to the attitude assumed towards them by the owners, bailiffs or gamekeepers of the different estates. When preserved in unfenced warrens their presence in neighbouring vegetation is naturally at its most severe pitch. These rodents, however, prefer a sandy soil, in which they breed, and if left alone, multiply rapidly. A clay soil on the other hand is unsuitable for their

colonisation and rapid multiplication. In this connection it is interesting to compare the damage done by rabbits on the sandy soil at Midhurst, with that caused by the same agents at Staffhurst Wood on clay and loam (Tables X and XIII). For this comparison I shall include those with "tips off" and those "missing" as being largely due to rabbit agency. The total for the Midhurst plots is 60.2 per cent. and for the Staffhurst plots 17.3 per cent., figures which in a general way show the greater efficacy of rabbits as destructive agents on sandy soil than on a clay soil.

The percentage lost through the agency of birds is not large. In their case evidence of their pecking in the soil in search of the acorn reveals the agent responsible, and I have known jays peck out acorns in this way. If the root has a firm hold of the soil, the acorn will be detached, leaving the seedling behind.

The above data clearly show the efficacy of animal agency in reducing the number of seedlings. These tables are compiled from observations made up to January 1916. Owing to absence abroad I was unable to visit the plots again until January 1919. The last column shows the number of seedlings then alive on plots which did not coincide absolutely with the original ones, as the stakes, which were utilised for marking off the areas and were chosen so as to minimise as far as possible any interference from outsiders, had all decayed and were indistinguishable from fallen branches. But in every case an area as nearly as possible coinciding with the original one was examined, with the results as entered in the last column. In the exposed areas on sandy soil only 1 per cent. remained, in the partially protected 6.4 per cent. and in the fully protected 27 per cent. On clay, unprotected, 8.5 per cent. remained. These figures represent the remnant after nearly 4 years from all causes operating against the seedlings' establishment. On account of my absence no data could be obtained as to the fate of these now missing, but the data available are quite sufficient to prove the efficacy of animals as agents militating against successful regeneration of oakwoods, especially on sandy soils.

Supplementary evidence as to the value of protection from animals was patent from observations made in the New Forest towards the end of August. Among such spiny plants as *Ilex Aquifolium*, *Prunus spinosa*, *Crataegus monogyna*, etc., usually near the periphery of clumps of these, saplings of various heights were found growing up among the protecting branches. Their demands for light led them to incline their stems to the outside of this protection but rarely did I find any protruding twigs which would be liable to be nibbled by the cattle, ponies, sheep, deer, etc., which roam through the Forest, or if they do project they are promptly eaten back. Once these branches emerge from this protection sufficiently high up to escape the browsing animals, the future of the tree is assured. It is no uncommon thing to find a large oak standing in the centre of such a clump—an oak which has grown up with the thorny species, the latter affording it the necessary protection. This

phenomenon has been recorded by numerous observers¹ for trees in general and undoubtedly the protection thus afforded was the salvation of the oaks in question. There were also in the Forest some oaks with a stem about $\frac{3}{8}$ in. in diameter and a bushy crown, growing among heather and whose height was the same as that of the surrounding vegetation. The small stature and bushy form were no doubt due to the continual browsing of animals upon the young shoots which projected above the level of the surrounding vegetation. Further, under the protection of spiny plants oaks may colonise new ground in progressive scrub². At Petworth on a piece of waste land, overgrown with tall gorse, there are a few oaks coming up, their foliage adequately safeguarded against animal attacks, whilst the acorn may also have escaped the smaller animals owing to the spiny medium of fallen thorns not being conducive to their comfort. Pounded gorse has been recommended³ as a protection against these.

When natural regeneration is found in certain areas the absence of some of the animals above mentioned usually accounts for it. One of the most successful examples of natural regeneration in the South East of England may be seen at Petworth, where on a particular estate rabbits are treated as vermin. Part of an oakwood was felled and enclosed against the roe deer present on the estate. No greater testimony to the value of protection can be had than to compare the part enclosed with the unenclosed. In the former regeneration is proceeding normally, while in the latter no saplings are seen at all or if so they are small and kept down. Here as in other places the presence of the workmen for a period may have helped to frighten away the animals and the general absence of vegetation which may attract them, for a year or so, probably also assisted towards the preservation both of the acorns and the seedlings.

The effect of a fungus (Oidium quercinum?).

In the above tabulated data there are columns set aside for the "dead" and "diseased," but as already remarked the vast majority of the seedlings, no matter where examined, showed the presence of a fungus. This fungus is one of the mildews provisionally called *Oidium quercinum*, as so far perithecia have not been found. More recent examinations⁴ of the conidia do not identify this fungus with the *Oidium quercinum* of Thümen, but as the matter is still unsettled I shall adhere to the provisional name given above. Attention was called to this fungus during the last quarter of the preceding century and more recently in Britain. The disease was observed on oak seedlings in woods throughout the South of England from Kent to Dartmoor and in the Forest of Dean. It occurred on plants on all varieties of soils and under all conditions as to light, e.g. from the heavy clay of the Weald to the light sandy soils at

¹ E.g. **Adamson**, *Proc. Linn. Soc.*, 1911, p. 339, **Tansley**, *op. cit.*

² **Adamson**, *op. cit.*

³ **Elwes** and **Henry**, *op. cit.*

⁴ **Griffon** and **Maublanc**, *Bull. de la Soc. Myc. de France*, 1910.

Midhurst and in the New Forest, as well as in those oakwoods degenerating to heath. It occurred likewise on seedlings exposed to full sunlight and on those under dense shade. The apparent effects of the fungus differed, however, in the various situations, but, as from my experiments it was impossible to determine what contribution the diminished supply of light paid and what the fungus paid towards the death of the seedling, in dealing with these two factors separately, this must be borne in mind.

Comparing the plots enclosed from animals (Table XII) where the somewhat heterogeneous column of "missing" is reduced to a minimum, we find that in plot 3 out of a total of 333 seedlings under dense shade, 266 are classed as dead or diseased, whilst in the other two plots there are only 2 reported dead. It may here be recalled that the column "diseased" includes only those which were suffering badly and were likely to die, whilst so long as the leaves remained turgid, the plants to which they belong are classed as "normal." Both the latter plots were exposed to full sunlight during 1915. Further, of those plots fully exposed to animals Nos. 1 and 2 were under dense shade. Out of the total number of seedlings in these two plots (57) 27 are classed as dead and diseased (= about 47 per cent.), whilst of the remaining seedlings in the other plots (604) only 23 are so classed (= about 4 per cent.). Further, in plot 1 of those protected, after 3 years the seedlings were from 2-3 ft. high, while in plot 2 they were only 9 ins. high; and here it is necessary to explain that bracken grew up uninterrupted during those years and shaded the seedlings. So that seedlings even although diseased can withstand the effects of this fungus and grow normally when supplied with sufficient light. How much of this diminished growth was due to the deficiency of light supply and how much was due to the disease acting more powerfully on a plant rendered less vigorous by growing in shade, cannot be determined from the above. Further experiments in this direction are required.

If we compare the seedlings under an open canopy on heavy clay soil with those on light soils under similar conditions the plants on the former seem of darker colour and more healthy than those on the latter. Yet a comparison of the exposed plots on sand with those on clay does not at first glance bear out this observation, for in the former 7.5 per cent. were dead or diseased while in the latter 6.4 per cent. were in a similar condition. If however we take into account the heavier mortality that has taken place in the former through animal agency, and consider those which are still exposed to the disease by comparing the normal with the diseased in both sets we arrive at the following:

On Sand. 7.5 per cent. dead and diseased while 14.2 per cent. remain normal.

On Clay. 6.4 per cent. dead and diseased while 40.1 per cent. remain normal.

This shows that up to my last observations the disease had more effect on seedlings growing on sand than on clay.

The fungus first appears on the leaves, which, upon the attack spreading, ultimately wilt. It thereafter attacks the shoot itself. Diseased leaves usually fall off so that in many cases where at first no seedlings are apparent, a closer examination reveals them quite stripped of their leaves with nothing but the shoot left, and even of this the tip is often diseased. Such seedlings, drawing on their reserves, often put forth new shoots, but the young leaves are immediately attacked and quickly succumb. This cannot continue, so the plant dies.

The effect of light.

For lack of exact experiments and data, opinions may differ as to the amount of light required by young oaks, but all agree that it is a "light demander" throughout its whole life history. Gordon¹ conducted a series of experiments where "an attempt is made...to determine more or less accurately the conditions most favourable to the development of advance growth (i.e. oaks from the seedling to the pole stage growing in association with the parent trees), in other words to determine approximately the optimum conditions for natural regeneration"; and his conclusions are in agreement with the generally established idea. "Long experience has shown that for the oak the lightest possible shade of seed bearers is compatible with most successful natural regeneration."

Now it has been recorded by Woodhead² that bracken often marks the site of degenerate woodland and ecologists testify to the frequency of this fern on sandy soil especially in the opener parts of woods. If we neglect the effects of the fungus and base our conclusions on the above established principle, then it seems clear that where bracken colonises the floor of a wood, the light supply will be cut off from the seedlings. Those seedlings I have observed under bracken were, at 4 years old, from 6-9 ins. high, while the last 2 or 3 years' growth was limited to $\frac{1}{2}$ in. or thereabouts in each year—seedlings which put forth their leaves and probably assimilated enough food to keep them alive before the bracken fully expanded its fronds (early June in S. of England) and cut off the supply of light. In these experiments there was no question of toxic action³ produced by the decaying fronds overlying the seedlings, as the fronds, becoming entangled in the wire netting overhead, remained suspended. Under such conditions the seedlings cannot survive indefinitely and eventually die. Where the bracken is very sparse I have seen in an enclosed area the seedlings 18 ins. to 30 ins. high during a like period.

Bracken, however, may act in another way. If the crop is dense the heavy rains and winds may cause it to become "lodged," when the bracken drags

¹ *Trans. of Scot. Arb. Soc.*, Vol. xxv. p. 147, 1912.

² *Journ. Linn. Soc.*, 1906, p. 333.

³ H. Jeffreys, E. P. Farrow, *Journ. of Ecology*, 5, pp. 145 and 165 respectively, 1917.

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down any young growth that still persists. Seedlings thus treated lie flat on the ground and under such conditions regeneration is impossible. An example of this may be seen at Petworth where in the enclosure (previously mentioned) part of the area shows saplings 10–12 ft. high while the area with a dense crop of bracken reveals few plants and these have assumed the attitude above described. In this case bracken may have had a toxic effect in reducing the number of seedlings, but, as previously pointed out, it can cause the death or dwarfing of the latter by simply cutting off the supply of light.

Where little or no bracken was present, as in Staffhurst Wood on clay, the supply of light which reached the ground was evidently insufficient to induce normal growth, for there also the surviving seedlings were only from 6–10 ins. high.

The effect of a leaf-eating agent.

On the majority of the seedlings observed in certain plots and on many in others, the leaves were observed to be eaten. Either pieces were taken from the edge of the leaf or holes were cut from its surface. The seedlings attacked worst in this way occurred either among humus or among grass, but this is not invariable, as under both conditions in some plots the leaves either remained entire or were scarcely touched. Plants under dense shade appeared to suffer less in this way than those under an open canopy. For example 2 plots, where records were kept of the numbers of plants thus affected, showed 25 per cent. attacked under dense shade, while two others under an open canopy showed 75 per cent. Further, out of a total of 248 seedlings in the plots at Staffhurst Wood on clay 42 (= 17 per cent.) were recorded as having their leaves eaten, a much smaller percentage than the average with leaves thus attacked on sand. On the plots fully exposed to light, where the parent trees had been felled the previous year, the seedlings were characteristically unaffected in this way. Generally speaking, for all the plots examined do not bear out the above deductions, the agent responsible apparently occurred in greater numbers where vegetation was present and was also more prevalent on sandy soil than on clay, being almost entirely absent where the soil had been consolidated by the woodmen in both felling and planting operations.

The damage done is similar to that of the earwig on Dahlias; and although I have examined numerous seedlings for any animals likely to cause this I failed to discover any. Most probably the agent, whatever it is, is nocturnal in its habits, retreating during the day into the soil. Few deaths can be assigned to this cause, but, by a reduction in the manufacturing parts of the vegetative tissue, effects reacting upon the seedlings' vitality are undoubtedly caused, e.g. the fungus previously mentioned would be more deadly on a plant whose vitality was thus impaired, where the full benefit of the available light supply could not be taken advantage of on account of the reduced leaf surface.

The influence of other factors.

Other causes undoubtedly affect the plant's welfare in this way, e.g. the occurrence of galls both on the leaves and the roots, and the presence of a coccid on the shoots must reduce the capacity of the seedlings to resist the attacks of disease, or to hold out where the light supply is none too abundant. But the occurrence of these is not general and at the most only a very small percentage of deaths can be attributed to these causes compared with the mortality due to the causes mentioned previously.

INTERFERENCE WITH THE BALANCE OF NATURE.

In the present investigation it is pertinent to ask why regeneration was successful in former days and successful now only in isolated places. Were acorns devoured in such wholesale quantities then as now and did as many seedlings disappear?

Apart from those factors considered in Part II, and apart from disease, the chief causes of the failure of natural regeneration of the oak are herbivorous animals. Has there been an increase in the number of these since primeval days, especially of rabbits and the smaller animals? We have no exact statistics of the animal population of any wood, but that there has been a general increase in the number of rabbits, mice, voles, certain birds, etc. may be gathered from the following considerations.

Carnivores feed on various animals, including herbivores, and herbivores feed on vegetation. Man, when he became a stock breeder, a keeper of herbivores, or of fowls, found it necessary for the more rapid multiplication of his flocks and herds to reduce loss as much as possible. Hence he became the enemy—if he had not already an instinctive hatred of carnivorous animals—of all such as preyed on cattle, sheep, pigs, fowls, etc. Not only did he protect his flocks from the inroads of these carnivores but he waged war, carrying it into his enemy's own country, with the result that certain of these have become extinct or nearly extinct in our island, and against those which still survive a bitter war is carried on.

More recently the rearing of birds for game has intensified the struggle and carried wider afield this warfare against all such animals as destroy or are reputed to destroy the game. The protection of these birds is left in the hands of the gamekeeper who, whatever interests are affected thereby, performs his duty only too efficiently by suppressing those animals which destroy young pheasants, etc.

Further, many carnivores are trapped for the sake of their skins, and the pursuit of this occupation tends still more to reduce their numbers. Similarly with many of our birds of prey, which are shot either for decorative purposes or because they destroy game, or at least have such charges imputed against them.

Now the herbivorous animals and birds, whether domesticated or wild, not being molested to so great an extent by their natural enemies, multiplied in proportion and in peopling the soil eat or destroy whatever vegetation is suitable to supply their wants. In this way the increase of destructive agents may be accounted for.

The following is a list of animals which prey on mice, rabbits, birds, etc., and their names arouse at once a feeling of animosity in the popular mind, so general is the belief that they are inimical to man's welfare, or to the increase of his wealth.

Enemies of mice, rabbits, pheasants¹, etc.: Owl, Buzzard, Gull, Rook, Black Crow, Hooded Crow, Kestrel, Polecat, Stoat, Weasel, Fox, Marten, Badger, Hedgehog, Shrew.

Man, by upsetting the balance of nature, and assuming control of what directly affected his own interests, is now paying the penalty in other ways, and must, having killed or suppressed the controllers, either assume total control himself or assist in such by a judicious encouragement of those animals he once considered his inveterate foes. "Civilised man has proceeded so far in his interference with extra-human nature, has produced for himself and the living organisms associated with him such a special state of things by his rebellion against natural selection, and his defiance of Nature's pre-human dispositions, that he must either go on and acquire firmer control of the conditions or perish miserably by the vengeance certain to fall on the half-hearted meddler in great affairs²."

SUMMARY.

In the light of the foregoing what measure of success in natural regeneration may we expect to be found in the different oakwood associations?

The importance of certain animals in the economy of the woodland has been pointed out in connection with the disappearance of both the acorn and the seedling. The prevalence of certain of these animals is in large measure, of course, dependent on local circumstances, e.g. on the attitude assumed towards them by the proprietors of the various estates. Pheasants for example may to a greater or less extent be thus limited. But in the case of the rabbit, natural circumstances favour its increase on sandy soils, so that the damage done on soils of this kind is greater than on clay soils. From the data available mice do not seem to be restricted in this way, so we may assume their ravages to be fairly evenly distributed over the various types of soil.

The importance of concealment to the survival of the acorn and the value of a humus layer in this connection are pointed out. The latter occurs more abundantly in the Damp Oakwood than in either the Dry Oakwood or Oak-birch-heath associations.

The relation of germination to the type of seed bed provided is also

¹ Nisbet, Schlich, *opp. cit.*

² Lankester, *The Kingdom of Man*, p. 31, 1907.

discussed and it is pointed out that while generally no inherent difficulties are met with to prevent natural regeneration in the Damp Oakwood, seed beds of an unfavourable kind became more frequent as we pass from the Dry Oakwood to the Oak-birch-heath associations.

The efficacy of the mildew in producing fatal effects on oak seedlings is shown to be greater on sandy soils than on clay, and the bracken, by its increasing frequency in the Dry Oakwood and Oak-birch-heath associations, by greatly diminishing the supply of light and impairing the vitality of the seedlings, materially assists the fungus in producing these effects.

Summing up one can say that the chances of success decrease as we pass from the Damp Oakwood association to the Dry Oakwood and from the latter to the Oak-birch-heath—a fact to be taken into consideration by the forester when he contemplates the natural regeneration of his oakwoods.

In conclusion, to Mr Tansley, who suggested the subject to me and who helped me throughout by kindly criticism, advice and discussion, I am especially indebted. To Mr Roberts and Mr McKenzie, foresters on the Cowdray and Didlington Estates respectively, I am also indebted for the interest they showed and the assistance they gave in the carrying out of some of the experiments. Finally I acknowledge my obligation to the Carnegie Trustees for the financial assistance necessary to carry out the work.

A PRELIMINARY NOTE ON THE ECOLOGY OF PART OF THE SOUTH LINCOLNSHIRE COAST

BY L. F. NEWMAN AND G. WALWORTH.

THE following notes are the result of a survey carried out by the authors at the request of the Land Reclamation Board. The Board have kindly granted permission for separate publication of the data obtained pending a further investigation of the more important points of interest suggested by the results.

The salt marsh and sea-wall surveyed stretch from Gibraltar Point on the north to the mouth of the River Witham below Freiston shore on the south. The strip of marsh varies from about 200 yards to nearly a mile in width, extending along the coast for 17 miles. The sea-wall separates the marsh from reclaimed silt, which forms exceedingly fertile land, and consists of an earth bank 20 yards wide at the base and 15—20 feet high. It was constructed about 70 years ago when the last enclosure on a large scale took place.

In *Types of British Vegetation* (pp. 330 et seq.), salt marsh is divided into five associations, but it was found that the district in question could not be mapped on this basis, especially for the purpose of the Reclamation Board. The zones or associations finally adopted were very well defined and constant in type.

The lists of plants identified in each zone and also from a pasture and meadow adjacent to the wall on the landward side indicate the species occurring in the months of July—August.

(A) *Bank zone*: the sea-wall, with a settled type of pasture vegetation closely fed by sheep. In the north this was a well-established mixture with *Lolium perenne* and *Arrhenatherum avenaceum* as dominants. In the south it passed to typical calcareous clayland pasture, but throughout the length of the wall calciphilous plants commonly occurred. For purposes of convenience a division was made at Wrangle (about midway) as this point marked a natural separation of the types mentioned.

(a) *Part extending N. of Wrangle.*

<i>Hordeum murinum</i>	<i>Aira flexuosa</i>	<i>Luzula campestris</i>
<i>H. arenarium</i>	<i>Glyceria maritima</i>	<i>Carex Goodenowii</i>
<i>Cynosurus cristatus</i>	<i>Lolium perenne</i>	<i>Juncus Gerardi</i>
<i>Arrhenatherum avenaceum</i>	<i>Festuca rubra</i>	<i>Ranunculus acris</i>
<i>Spartina stricta</i>	<i>F. duriuscula</i>	<i>R. repens</i>
<i>Agropyrum junceum</i>	<i>Dactylis glomerata</i>	<i>Senebiera Coronopus</i>
<i>Poa annua</i>	<i>Bromus mollis</i>	<i>Cochlearia officinalis</i>

<i>Capsella bursa pastoris</i>	<i>Cnicus lanceolatus</i>	<i>Plantago lanceolata</i>
<i>Cerastium tetrandrum</i>	<i>C. arvensis</i>	<i>P. Coronopus</i>
<i>Spergularia salina</i>	<i>Carduus nutans</i>	<i>P. maritima</i>
<i>Malva sylvestris</i>	<i>Bellis perennis</i>	<i>Salicornia</i> spp. (annua type)
<i>Geranium molle</i>	<i>Achillea millefolium</i>	<i>Suaeda maritima</i>
<i>Lotus corniculatus</i>	<i>Artemisia maritima</i>	<i>Obione portulacoides</i>
<i>Trifolium repens</i>	<i>Crepis virens</i>	<i>Atriplex hastata</i>
<i>T. pratense</i>	<i>Hypochaeris radicata</i>	<i>A. littoralis</i>
<i>T. minus</i>	<i>Taraxacum officinalis</i>	<i>Polygonum aviculare</i>
<i>Medicago lupulina</i>	<i>Glaux maritima</i>	<i>Urtica dioica</i>
<i>Galium verum</i>	<i>Armeria maritima</i>	<i>Triglochin maritimum</i>

(b) *Part extending S. of Wrangle.*

The same species occurred as in (a) but with the following additions:

<i>Phragmites vulgaris</i>	<i>Trifolium procumbens</i>	<i>Leontodon hispidus</i>
<i>Aira caespitosa</i>	<i>Daucus carota</i>	<i>L. autumnalis</i>
<i>Holcus mollis</i>	<i>Caucalis nodosa</i>	<i>Sonchus oleraceus</i>
<i>H. lanatus</i>	<i>C. Anthriscus</i>	<i>Limonium vulgare</i>
<i>Agropyrum repens</i>	<i>Chaerophyllum sylvestre</i>	<i>Primula veris</i>
<i>Briza media</i>	<i>Galium Aparine</i>	<i>Rhinanthus Crista-galli</i>
<i>Linum catharticum</i>	<i>Aster Tripolium</i>	<i>Plantago media</i>
<i>Geranium dissectum</i>	<i>Senecio vulgaris</i>	<i>P. major</i>
<i>Vicia sepium</i>	<i>S. Jacobaea</i>	<i>Rumex Acetosa</i>
<i>V. Cracca</i>	<i>Centaurea nigra</i>	<i>R. sanguineus</i>
<i>Lathyrus pratensis</i>	<i>Tragopogon pratensis</i>	

It will be seen from the above lists that the bank flora includes a considerable number of calciphilous species, especially on the southern portion of the bank, and this was emphasised by the fact that such species as *Reseda luteola* and *Ononis spinosa* occurred behind the wall. Nearly all the land behind the bank is under arable cultivation, but near Wrangle two grass fields were found, one of which was a derelict pasture and the other a meadow cut for hay. The following plants were identified in these:

Pasture

<i>Holcus mollis</i> d.	<i>Ranunculus repens</i>	<i>Taraxacum officinalis</i>
<i>H. lanatus</i> d.	<i>R. acris</i>	<i>Senecio Jacobaea</i>
<i>Lolium perenne</i> d.	<i>Sinapis nigra</i>	<i>Crepis virens</i>
<i>Plantago lanceolata</i> d.	<i>Cerastium vulgatum</i>	<i>Hypochaeris radicata</i>
<i>Cynosurus cristatus</i> d.	<i>Potentilla anserina</i>	<i>Anagallis arvensis</i>
<i>Lotus corniculatus</i> d.	<i>Linum catharticum</i>	<i>Prunella vulgaris</i>
<i>Aira caespitosa</i>	<i>Medicago lupulina</i>	<i>Juncus articulatus</i>
<i>A. flexuosa</i>	<i>Trifolium repens</i>	<i>Carex Goodenowii</i>
<i>Dactylis glomerata</i>	<i>T. pratensis</i>	<i>Equisetum arvense</i>
<i>Bromus mollis</i>	<i>T. minus</i>	<i>Agropyrum junceum</i> *
<i>Arrhenatherum avenaceum</i>	<i>Galium verum</i>	<i>Vicia sepium</i> *
<i>Festuca rubra</i>	<i>Bellis perennis</i>	<i>V. Cracca</i> *
<i>F. ovina</i>	<i>Cnicus arvensis</i> (white form)	<i>Daucus carota</i> *
<i>Poa pratensis</i>	<i>C. lanceolata</i>	<i>Urtica dioica</i> *
<i>Hordeum murinum</i>	<i>Achillea millefolium</i>	

* Occurring on bank of pasture.

Meadow cut for hay.

Phleum pratense d.	Lolium perenne	Trifolium repens
Holcus mollis d.	Hordeum murinum	Taraxacum officinalis
H. lanatus d.	Bromus mollis	Cnicus arvensis
Dactylis glomerata d	Ranunculus repens	Plantago major
Cynosurus cristatus d.	Trifolium pratense	P. lanceolata

(B) *Bank base zone.* Along the seaward base of the wall a narrow strip 10—20 feet wide formed a well-marked zone with *Agropyrum junceum* and *Spartina stricta* as dominants: a similar association was found in small scattered patches over the marsh, wherever an elevation of two feet or so occurred, especially along the upper margins of the low cliffs (also about two feet in height) which apparently arose from the erosion of higher areas. Although *Agropyrum junceum* is very coarse these patches were subject to attack by sheep and cattle. All these areas were grouped together and mapped as "bank base zone." They are only liable to infrequent submergence.

Dominants.

<i>Agropyrum junceum</i>	<i>Festuca rubra</i>
<i>Spartina stricta</i>	<i>F. ovina</i>

Occurring generally.

<i>Cochlearia officinalis</i>	<i>Carduus nutans</i>	<i>Atriplex hastata</i>
<i>Spergularia salina</i>	<i>Artemisia maritima</i>	<i>A. littoralis</i> v. <i>genuina</i>
<i>Cnicus arvensis</i>	<i>Armeria maritima</i>	<i>Glaux maritima</i>
<i>C. lanceolata</i>	<i>Obione portulacoides</i>	

On trodden parts of bank.

<i>Lolium perenne</i>	<i>Poa annua</i>	<i>Senebiera Coronopus</i>
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Occasional.

<i>Salicornia</i> spp. (annua)	<i>Suaeda maritima</i>
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(C) *Festuca rubra zone.* A well-marked area with *Festuca rubra* as dominant associated with much *Spergularia salina* and *Glaux maritima* forming flat lawn-like patches only submerged at specially high tides and closely grazed by sheep. This association was mainly restricted to the northern end of the marsh.

Dominants.

<i>Festuca rubra</i>	<i>Spergularia salina</i>
<i>F. duriuscula</i>	<i>Glaux maritima</i>
<i>F. ovina</i>	

Occurring generally.

<i>Cochlearia officinalis</i>	<i>Plantago maritima</i>
<i>Armeria maritima</i>	<i>Aira caespitosa</i>
<i>Artemisia maritima</i>	<i>A. flexuosa</i>

Occurring occasionally.

<i>Limonium vulgare</i>	<i>Obione portulacoides</i>
<i>Triglochin maritimum</i>	<i>Salicornia</i> spp. (annua)
<i>Suaeda maritima</i>	

This zone mainly covered the better drained parts of the marsh. It is usually fairly heavily sheeped and, generally speaking, was on the more sandy areas. Where *Obione* did occur it was restricted to the small pools and water channels.

(D) *Intermediate zone*. Areas of intermediate vegetation showing many of the characters of the *Festuca* zone but containing abundant *Obione portulacoides* so that *Festuca* and *Obione* were equal dominants. The plant association was however fairly constant in type and warranted separation as an intermediate zone.

Dominants.

<i>Festuca rubra</i>	<i>Obione portulacoides</i>
<i>F. duriuscula</i>	<i>Suaeda maritima</i> s.d.

Occurring generally.

<i>Glyceria maritima</i>	<i>Armeria maritima</i>	<i>Aster Tripolium</i>
<i>Agropyrum pungens</i>	<i>Limonium vulgare</i>	<i>Glaux maritima</i>
<i>Artemisia maritima</i>	<i>L. reticulata</i>	<i>Salicornia</i> spp. (annua)
<i>Spergularia salina</i>	<i>Triglochin maritimum</i>	<i>Plantago maritima</i>

Triglochin maritimum, *Limonium vulgare* and *Aster Tripolium* were rather rare in the northern part of the marsh, but at the southern end (Freiston) they became sub-dominants.

Salicornia spp. ("annua") increased seawards until they passed into the "*Salicornia-Festuca* zone."

Obione was mainly restricted to the water channels and pools, otherwise in small isolated colonies.

Artemisia occupied little elevated hummocks wherever they occurred, whilst the larger hummocks and cliff edges passed back into typical "Bank base zone."

(D 1) *Festuca-Agropyrum zone*. This occurred at the southern end of the marsh on water-logged areas, and was marked by the equal dominance of *Festuca rubra* and *Agropyrum pungens*.

Species of D (*Intermediate zone*) occurred in very small numbers.

(E) *Obione zone*. Areas of almost continuous *Obione portulacoides*.

<i>Obione portulacoides</i> d.	<i>Suaeda maritima</i> s.d.
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Occurring generally.

<i>Festuca rubra</i>	<i>Triglochin maritimum</i>
<i>F. duriuscula</i>	<i>Limonium vulgare</i>
<i>Aira flexuosa</i>	<i>Aster Tripolium</i>
<i>Glyceria maritima</i>	

Occurring occasionally.

<i>Spergularia salina</i>	<i>Armeria maritima</i>
<i>Cochlearia officinalis</i>	<i>Plantago maritima</i>
<i>Salicornia</i> spp. (annua)	

This was the most extensive zone, large areas being covered with a thick almost continuous mass of *Obione*, the other plants of the zone only occurring in patches. The *Obione* passed practically down to normal tide limit in most of the areas occupied, thus indicating the great powers of resistance to sea water submergence.

It would appear that for purposes of land reclamation, *Obione* zones present considerable difficulties, for the herbage is coarse, practically uneatable by sheep and possessing tough perennial root-systems.

(F) *Festuca-Salicornia* zone. At about average high tide level a well-defined band of *Festuca rubra* in clumps with *Salicornia* spp. growing between.

<i>Festuca rubra</i> in clumps d.	<i>Limonium vulgare</i> o.
<i>Salicornia</i> spp. between the clumps d.	<i>Plantago maritima</i> o.
<i>Suaeda maritima</i> s.d.	<i>Obione portulacoides</i> o.
<i>Aster Tripolium</i> o.	Algae spp. o.

This zone formed a narrow band round high tide level, being a connecting link between the *Salicornia* zone and the real herbage areas. It passed into the *Intermediate* and *Obione* zones and appears to indicate that *Festuca* forms are more resistant to tidal action and sea water submergence than any other type of marsh plant with the exception of the *Salicornias*. The area included in this zone is much broken by tidal action and water channels, and consists of a series of small clumps of almost pure *Festuca* with *Salicornia* between the clumps.

(G) *Salicornia* zone. This consisted of species of *Salicornia* pure or nearly pure.

<i>Salicornia</i> spp. d.	<i>Festuca rubra</i> r.	Algae spp. r.
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The following forms of *Salicornia*:

A. *Perennial forms*:

Salicornia radicans
S. lignosa

B. *Annual forms*:

Salicornia annua
S. ramosissima

Moss¹ records no perennial forms of *Salicornia* farther north than Norfolk, but two distinct areas of perennial spp. were discovered, one at the extreme north and the other at the extreme south of the area under survey. Typical specimens of both *S. radicans* and *S. lignosa* were removed. Very diverse types of *S. annua* were noted, including a small bright scarlet form, but the writers consider the present classifications of annual *Salicornias* are too indefinite to venture any further separations than the above.

The zone occupies the mud flats and varies considerably in width. It lies beyond the "true vegetation limit" as defined by the Ordnance Survey and fringes the whole length of the marsh.

¹ *Cambridge British Flora*, Vol. II. p. 189.

(H) *Algae-Zostera* zone. A narrow strip about a quarter of a mile below high tide and well beyond the "*Salicornia* zone" is covered with patches of varying density. These consist of *Zostera marina*, *Z. nana* and associated algae. Further observations will be necessary to provide a complete list of the forms occurring here.

As is usual in maritime marshes the number of species is restricted, but the ground is covered with vegetation down to, and in some cases below, the ordinary tide line.

The marsh is liable to flood at the highest tides of the season right up to the bank, but the ordinary high tides just wash the outer fringe of vegetation above the *Salicornia* zone, while at low tides a strip of silt or mud varying in width from one to four miles is left exposed.

The salt marsh is irregularly dotted with shallow pools replenished at spring tides and is more or less drained by a series of dykes or ditches empty at low tide but filling up with the flood and carrying off the water at the ebb.

The following analyses of soils taken from the various zone areas were carried out by Mr E. J. Roberts of the School of Agriculture, Cambridge, who kindly supplied the figures from his data.

	Salicornia zone Friskney		Obione zone Freiston		Intermediate zone Wrangle		Festuca zone Friskney	
	topsoil	subsoil	topsoil	subsoil	topsoil	subsoil	topsoil	subsoil
<i>Mechanical</i>								
Fine gravel	—	—	—	0.01	—	—	—	—
Coarse sand	0.05	0.05	0.10	0.01	0.15	0.05	0.20	0.05
Fine sand	84.80	84.30	20.75	35.80	37.95	40.25	38.75	55.35
Coarse silt	1.65	1.35	16.05	15.40	20.30	21.50	15.63	10.60
Fine silt	0.95	1.15	9.83	10.28	11.65	9.58	10.33	7.26
Clay	1.14	1.19	20.58	20.18	13.48	13.98	13.38	9.93
Loss on ignition	3.20	3.40	11.65	9.13	9.50	5.90	8.00	5.90
Residual moisture	0.50	0.40	2.13	1.56	1.80	1.60	2.70	1.30
<i>Chemical</i>								
Nitrogen	0.034	—	0.212	—	0.281	—	0.165	—
Potash	0.221	—	0.836	—	0.646	—	0.666	—
Phosphorus pentoxide	0.056	—	0.088	—	0.090	—	0.072	—
Calcium carbonate	8.325	—	11.00	—	2.65	—	9.10	—
Sodium chloride in parts per million in 1—5 soil solution	1292.5	—	2157.5	—	1665.0	—	1260.0	—
Insoluble in strong hydrochloric acid	84.75	—	66.13	—	75.69	—	71.75	—

The information obtained from the preliminary survey of the marsh has indicated several important points which need further investigation and also a series of observations at other periods of the year when the plant lists could be extended and completed for the whole year. The main points of interest to be elucidated are:

- (1) The relative stability of *Obione portulacoides*.
- (2) The types of plants most suitable for silt collection.

- (3) The relative fertility of the different zone areas.
- (4) The relative power of invasion of the zones indicated.
- (5) The relation of the associations to the underlying soils.

The soil analyses show a high percentage of calcium carbonate and this is reflected in the vegetation especially on and near the sea-wall. The relative proportion of sand and nitrogen in the *Salicornia* zone and the more settled regions contrasts remarkably and illustrates the inability of *Salicornia* alone to hold up silt which *Obione* and *Festuca* appear to do successfully.

We regard the above survey as indicating the advisability of separating the accepted salt marsh associations into further subdivisions. These subdivisions although well marked and quite definite merge into each other and may indicate transitory stages in progression or retrogression of land and purely maritime plants. It appears that in this particular region the land flora is gradually gaining dominance over pure salt marsh vegetation as the land level rises, a condition that would be expected in the Wash area.

The authors are indebted to Mr F. Hardy who assisted in the survey as geologist; to Mr E. J. Roberts for permission to use examples from his detailed soil survey of the area, and finally to the Director of the Land Reclamation Board for permission to publish separately these notes of the survey undertaken by them for the purposes of the Board.

NOTICES OF PUBLICATIONS OF GENERAL BEARING

WOODLANDS AND NITRIFICATION

Hesselman, H. (1) "Studier över saltpeterbildningen i naturliga jordmåner och dess betydelse i växtekologiskt auseende." *Meddel. från Statens Skogsförsöksanstalt*, 1917, Heft. 13-14, p. 297.

(2) "Om våra skogsföryngringsåtgärders in verkan på saltpeterbildningen i marken och dess betydelse för barrskogens föryngring." *L.c.* 1917, p. 923.

(1) This paper is supplied with a *résumé* in German. It is a lengthy and important contribution to the ecology of woodlands. The problem attacked is that of the nitrogen in the soil in woodlands and its transformations to assimilable forms. The methods employed are partly bacteriological, and partly chemical tests on living plants. The soil was tested for nitrifying and denitrifying power in solutions and also its power of accumulating nitrates was measured. Tests were made for the presence of nitrates in shoots and leaves. Full tables of the results of the soil experiments are given. The paper commences with a general account of the nitrification of the soil in various types of Swedish vegetation. Lists are given for the various localities described, with frequencies appended. Also in each list the reactions of the tissues of the principal species are given.

Beech woods have a soil with a leaf mould type of humus. Nitrification is found to be constantly taking place and nitrates can be demonstrated in the tissues of many species in spring. Soil samples showed active nitrification and denitrification and stored samples accumulated considerable quantities of nitrate.

Mixed dicotyledonous woods with *Quercus*, *Carpinus*, *Ulmus*, *Fagus*, etc. also have a leaf mould type of humus. Nitrification is here very active—in some cases even more so than in Beech woods, especially in rather damp shady parts.

Woodmeadows (*Laubwiesen*) comprise a series of associations which contain in S. Sweden elements of the oak wood flora and that of much more open places. They are very rich floristically. In N. Sweden they differ in composition, *Betula*, *Alnus* and *Salix* being the chief woody plants and the herbaceous vegetation of much more subarctic description. However the physiognomic similarity is very great. The soil generally has a leaf mould character and shows active nitrification though less than in the previous types.

Ravine woods (*Hainälchen*) occur along the borders of streams. They are markedly nitrate forming and most of the plants show a marked reaction.

Alder woods are composed of *Alnus glutinosa* on the Baltic coast and of *A. incana* in N. Sweden. These were found to be the most markedly nitrate forming associations examined. The majority of the plants of the ground flora have a high nitrate content.

The *conifer forests* are divided into two types according to their type of ground flora—a “herbulent” type and a mossy type. Herbulent spruce woods occur especially on calcareous rocks and have a rich tall growing ground vegetation. The soil has a well-developed leaf mould humus. The plants however, even strongly nitratophilous species, seldom show any nitrate reaction, though nitrifying organisms are present. The accumulation of nitrate in stored samples is rather small. Pine woods of the same type are also described.

The mossy type of conifer forest with its monotonous ground flora of mosses and ericaceous undershrubs is however very much more abundant in N. Sweden. The humus here is a “raw” humus and forms a distinct layer on the surface. Where the ericaceous plants become important the humus becomes peaty in character. Under this humus is a layer of bleached soil of varying thickness overlying a rusty brown layer which however rarely has an “ortstein” character and is readily penetrable. The humus has a distinctly acid reaction. No nitrification occurs in solution here and denitrification also is absent. Stored samples also form very little or no nitrate, the amounts being below the limits of experimental error. The trees and plants in these woods must obtain their nitrogen either as ammonia or in an organic form.

Pine Heaths with a ground flora of lichens and heath plants showed a similar entire absence of nitrification.

Peat bogs (*Torfböden*) have a soil very unfavourable to nitrification with stagnant water and a strongly acid reaction. When the water is in rapid motion however nitrification can be found. Round springs and stream edges a nitratophilous flora occurs, in which nitrates can be demonstrated in the tissues. In lowland moors (*Niederungsmoor*), which however from the lists approach rather to marshes, nitrates can be found in plants by rapid flowing water. In dry drained peat active nitrification may occur.

Among examples of alpine vegetation some of the most active nitrification has been found especially by channels either from springs or water of melting snow.

Rock plants were found to possess in all cases a high nitrate content and the same is true of colonizing plants on bare mineral soils. A few observations on sea coast plants and culture associations also indicate a high nitrification power in the soil.

The various vegetation types show great constancy in regard to nitrification in various parts of the country. Further, in soils with active nitrification the plants tend to be autotrophic while when nitrification is absent they are mycotrophic (i.e. with mycorrhiza).

The whole question of soil acidity is closely associated with the form of nitrogen available, nitrates being physiologically basic and ammonium compounds acid, but the cause is something different as in certain acid soils nitrates are present.

Plants show very great variations in the nitrate content of their leaves and the absence of a reaction cannot be taken to indicate absence of nitrification.

Certain plants, called nitratophilous plants, show a decided tendency to accumulate nitrates, giving at times a strong reaction when the nitrification in the soil is very slow. Two of the most strongly nitratophilous plants are *Epilobium angustifolium* and *Rubus Idaeus*. Both plants have a wide range of light values and soil moistures, but a necessary condition for their existence is the power of the soil to build nitrates. Young plants always give a reaction but older ones do not. These and some other species act as a very valuable guide to the forester in estimating soil conditions.

Soils washed by flowing water nearly always show the nitrate reaction in plants, but storage of samples often shows no increase; when the sample is supplied with air kept in rapid motion a big increase occurs.

In sharp contrast to the nitrate forming soils are those of the mossy conifer woods. The climate of Sweden is markedly favourable to rapid leaching of the soil and the accumulation of raw humus: under those conditions no nitrification is possible and in the northern parts such conditions arise even when the underlying soil is calcareous.

This is especially so on level or very slightly sloping localities. On steeper slopes the leaching process is not so effective and a leaf mould type of humus results with the herbulent spruce woods with nitrification in the soil. The presence of lime in peat soils is generally evident and leads to a fen type of vegetation. Where peat is supplied with water containing lime, many calcicole plants appear, especially at the margins of swamps. An extreme case of this is figured, where *Cypripedium calceolus* is shown growing in a mass of *Sphagnum fuscum*.

In viewing the geographical distribution of the various plant communities, the importance of the local conditions leading to one or other of the various types of humus and its consequent power or otherwise of nitrification is very evident.

(2) The second paper, which has a *résumé* in English, is an extension of the work of the first one especially in relation to the problems of forest regeneration.

When forest is cut or an opening occurs and an increased illumination is admitted, a much more prolific and often much more varied flora appears. The causes certainly lie deeper than the admission of more light. The plants are very often those that accumulate nitrates in their leaves.

In the herbulent coniferous forest nitrate is found in the soil, but the formation is not active and none can be detected in the plants. Clearings however show a very vigorous growth, often so luxuriant as to prevent tree growth, and much nitrate can be found in the plants.

In the mossy conifer wood there is no nitrate formation. The humus forms a distinct crust on the ground and is acid. After a cutting changes occur, scattered nitratophilous plants occur and some nitrification can be found in the soil. Two years after cutting nitrification is vigorous, and humus becomes much more mould-like and less acid. This change is entirely independent of any preparation of the ground for a new crop.

In other forests, especially those of Norrland, quite different results follow felling. The humus here has a much more peat-like character and may be 7—9 cm. deep. *Vaccinium* is the chief ground plant.

The regeneration of these forests is an important economic question and neither clear felling nor select cutting has led to natural regeneration. The soil shows no nitrifying organisms and no nitrate is formed from ammonium sulphate. Denitrification is also absent. After cutting, *Deschampsia flexuosa* rapidly becomes dominant. The humus often lessens in quantity and becomes more mould-like but no nitrification results.

In the neighbourhood of old stumps or where brushwood has been left, plants of *Epilobium angustifolium* and *Rubus Idaeus* may appear. Mouldering timber favours the transformation of nitrogen to nitrate, though dry and slowly decaying branches have no effect. Exactly the same effects and the same appearance of these nitratophilous plants can be seen round small forest saw mills.

In the neighbourhood of upturned roots and where the mineral soil is mixed with the humus a nitratophilous flora appears, which gives strong nitrate reactions; the soil from such places was found to form nitrates. A preparation of the soil by a cultivator causing a mixture of humus with the underlying mineral soil leads to strong nitrification.

Forest fires are very common in these woods; so common indeed that it is difficult to find an area without charcoal remains in the humus. Both the species mentioned above are common on burnt ground. Burning causes a complete change in the bacterial flora, nitrification and denitrification become active, ammonium sulphate is oxidized to nitrate and larger quantities of ammonia are formed from peptones. The power of nitrification may be retained as long as 12—25 years, but is often lost quite soon.

Nitrate forming bacteria are evidently very widely distributed in nature, and where not found, the conditions are unfavourable for their development. Probably infection of the soil is continually going on but development is only possible under certain conditions. By comparison with the results obtained with *Azotobacter* which can only live in presence of bases, it seems reasonable to suggest that nitrifying organisms have similar demands. The results of the experiments seem to show that the presence of electrolytes is necessary for their development and this is adopted as a working hypothesis.

The effect of cutting and admission of light would thus not be due so much to the light itself as to the increase in oxidation and evaporation, both of which tend to produce electrolytes in the surface layers.

In the Norrland forests the introduction of electrolytes is much less, the mouldering of the humus is less, and owing to the much deeper layer of bleached sand below the soluble salts raised by evaporation are very much less. The question of how the salts work is at present purely in the position of a hypothesis.

It is well known to foresters, especially in the Norrland forests, that there is a very close parallelism between natural regeneration and nitrification in the soil, and wherever it has been shown that nitrification has been permitted regeneration occurs even under a dense canopy. In the herbulent forests the very vigorous growth is often too strong for the young trees, but regeneration is active in small gaps when the light restricts other plants. Where the nitrogen is not transformed to nitrate, natural regeneration is slow or absent: and young plants of pine or spruce grow very slowly. Again under these conditions regeneration demands a much greater degree of light. Some experiments have been carried out on the question of the demands of young trees. Young plants of *Pinus* in a soil that allows nitrification grow better, have longer annual shoots, longer and darker green needles, and are altogether larger and more healthy than those grown in humus with no nitrification. Exactly the same thing can be seen on comparing pine seedlings growing in natural woodlands. For *Pine* apparently the nitrification of the humus is of very great importance in early youth. The same holds good in the main also for Spruce. This tree is also more responsive to nitrates in mature life.

Nitrification is not an indispensable *sine qua non* for regeneration of conifer forests, but a very favourable factor.

Both papers are illustrated with a number of excellent photographs, very well reproduced as text-figures. Some of the photographs are so good that it seems a pity they are not on superior paper.

R. S. A.

INVESTIGATIONS ON SOIL, ROOTS, ETC.

Hartwell, B. L., Pember, F. R. and Howard, L. P. "Lime Requirement as determined by the Plant and by the Chemist." *Soil Science*, **7**, 1919, p. 279.

The experiments were carried out on four permanent plots at the Rhode Island station. In the experiments lime and fertilizers were added two weeks before planting. After maximal crops from liming had been obtained the soil still showed a requirement of 5000 lbs. and when this was made up by adding 4000 lbs., lettuce, a strongly acid-intolerant species, showed a depression in growth due to "acidity." Analyses showed that not more than 1 % of the lime remained as carbonate.

Limed soils showed little gain from addition of nitrate of soda. When lime requirement was completely made up lettuce showed less growth than when smaller amounts were added. Rye and barley are also affected by acidity but rye is not benefited by lime as much as barley. The plants were equally affected by soil solutions or by a solution of the ignited residue. This last was found to contain considerable quantities of aluminium. The addition of aluminium sulphate to nutrient solutions depressed the growth of seedlings considerably, much more with barley than with rye. The toxicity of aluminium sulphate is due to hydrolysis and consequent acidity. The hydrolysis in nutrient solution is sufficient to produce $\frac{1}{4}$ the hydrogen-ion concentration produced by the required acid.

The elimination of toxic effects of aluminium is much more important than the neutralization of acidity. It can be rendered inactive by an acid phosphate. Lettuces showed a marked reaction when this was done.

Growth of lettuces	Acid phosph. added	Lime requirement at close of expt.
0	0	8300
74	14 tons per acre	9000
272	28 " " "	12000
201	2 tons lime per acre	5800

Hibberd, P. L. "Changes in Composition of the Soil and of the Water Extract of the Soil following the Addition of Manure." *Soil Science*, **7**, 1919, p. 259.

Fresh horse manure was added in varying proportions to soil and analyses made at intervals up to 395 days. At each analysis the original manure in a 1 : 10 extract was examined and also a 1 : 5 extract of the soil.

The following were the chief results:

The CO_2 in the soil atmosphere was increased, especially at the commencement of the experiment. The amount was proportional to the amount of manure added.

The total carbon showed a decrease which was rather rapid and in proportion to the manure added. The total nitrogen does not vary within the limits of error of the experiment.

The total soluble material showed an immediate decrease in proportion to the manure added, followed by an increase, but at no time was the soluble material equal to the sum of that in manure and in soils. The decrease is especially in organic matter, potash and lime. The cause of this is obscure. The fixation differs with different soils; subsequent experiments with rotted manure showed much less. The nitrates almost disappeared immediately after mixing, but later showed a gain in amount, the gain being greater the greater the amount of manure added. This initial loss and subsequent gain is ascribed to biochemical activity. The effect of adding manure is not simply additive and the experiments do not indicate an increase in solution of calcium, magnesium, sodium and potassium due to changes

from organic to inorganic acids. The increase in water soluble material can be accounted for largely by that derived from the mineral matter in the manure. But the experiments were too short to show the whole effect.

Doddall, Louise. "Water Requirement and Adaptation in *Equisetum*." *Plant World*, **22**, 1919, pp. 1-29.

The water used by *Equisetum* has been compared with that of *Bryophyllum*, *Helianthus*, *Phaseolus* and *Ranunculus sceleratus*.

Owing to the depth of the rhizomes some difficulty was found in transplanting *Equisetum*. It was found best to dig up rhizomes in autumn and plant buds in pots. Potometer experiments were not successful. The wilting coefficient was determined by the method of Briggs and Shantz. This was done both with separate plants and by growing *Equisetum* in the same pots as mesophytes. The wilting coefficient readings were always higher than for the other plants and in the same pot experiments the horsetails uniformly wilted first.

The transpiration per unit area of *Equisetum fluviatile* is also higher than that of other plants, 2 to 4 times that of *Helianthus* and *Phaseolus* and 10 times that of *Bryophyllum*, while even compared with *Ranunculus sceleratus* the loss is greater in the value of 10 : 8 or 9. *Eq. arvense* loses $\frac{4}{10}$ and *Eq. hiemale* $\frac{1}{6}$ the amount of *Eq. fluviatile*. All three species showed vigorous guttation at the nodes.

When transpiration and assimilation are compared *Equisetum fluviatile* is found to transpire 1.5 times as much as *Helianthus* and 2.3 times as much as *Phaseolus*, but *Helianthus* builds 1.8 times the amount of carbohydrates and *Phaseolus* 3 times as much. The figures refer to equal areas. The guard cells of the stomata are found to be permanently open and to show no difference in light or darkness.

The species examined showed no structural adaptation with change of habitat.

The water requirement of *Equisetum* is relatively large and *Eq. fluviatile* can be regarded as a true hydrophyte. The xeromorphism is due to ancestral features.

Waterman, W. G. "Development of Root Systems under Dune Conditions." *Bol. Gaz.*, **66**, 1919, p. 22, 17 figs. [Contrib. Hull Bot. Lab. 250.]

The area on which the investigations were made is part of the sand-dune complex of Lake Michigan. The soil is a fairly homogeneous blown sand with a considerable percentage of calcium carbonate. It shows a very unequal distribution of organic matter formed by old soil levels and buried plant remains. Part of the carbonaceous material in the soil may be due to soot from steamers which accumulates on snow and is subsequently buried. The water content varies from a 2 % average on open dunes to 7.5 % on the underlying glacial deposits: the wilting coefficients are 0.5 % and 3.3 % respectively.

In studying the development of roots, seedlings and young plants were especially examined. The conditions of germination were also studied and some experiments carried out. From the studies of living plants *in situ* and under experimental conditions the difficulty of penetration of the soil never seemed a factor in root development, and except in the case of *Salix* spp. water content is not a causal factor. On the other hand chemical substances undoubtedly alter the root development. This is especially marked in the case of *Prunus pumila*. The seeds of this plant germinate when buried in 1-2 ins. of sand. The growth of the root system is generally asymmetric and irregular. The irregularities in nature are connected with the distribution of decayed or decaying plant remains in the sand. Lateral roots are larger and more branched in the dark layers and roots may even reverse their direction of growth when coming in contact with organic matter and

pass along it. The dead twigs etc. are not penetrated by the roots but around them numerous lateral branches are produced.

In experimental cultures much more free branching of the roots occurred when the pots were watered with Knop's solution than with water. Again if water is supplied through a porous cylinder containing Knop's solution there is a marked development of lateral roots in the zone of diffusion which is absent with controls supplied with distilled water. In a pot to which one patch of rotted manure was added there was a great development of roots just below the patch.

Artemisia caudata has also an asymmetric root system, but does not show such a sharp relation to organic materials. Its roots seem rather related to water supply and often show a high degree of parallelism with the surface.

Ammophila does not flourish when there is an appreciable amount of humus. The roots show little relation to organic matter, continuing their growth directions without reference to such patches. In seedlings the roots may be inhibited by organic matter, roots reaching a patch and not passing beyond.

Salix shows a vigorous positive hydrotropism. Several other species are described and numerous photographs of root systems are reproduced.

R. S. A.

THE QUADRAT METHOD

Weaver, J. E. "The Quadrat Method in Teaching Ecology." *The Plant World*, **21**, 1918, p. 267.

The quadrat method is of great educational value in demonstrating to students (1) the large number of species often present in a small area, (2) the number of individuals and consequent degree of competition, (3) life-histories by study at different seasons, (4) the form and appearance at different stages of development. The knowledge and impressions of vegetation ordinarily acquired are apt to be limited and static. The repeated visits and the close attention demanded in recording and studying quadrats teach, among other things, the high mortality among seedlings and the difficulties of ecesis, the ephemeral nature of certain species and the stability of others, the variations occurring from year to year, and above all the dynamic view of vegetation, the habit of logical reasoning and the value of scientific accuracy. Even when one year only is available to the student for the study of ecology the above-mentioned advantages can be gained by setting up permanent quadrats in different types of vegetation, making the students map them and supplying the students with the charts of previous years for careful comparison and analysis. In this way the reactions occurring in each quadrat can be discovered and understood by the student. Valuable results have been obtained in ruderal areas with quadrats mapped at intervals throughout the season, and this exercise is particularly useful to students whose taxonomic knowledge is limited. One such quadrat contained 10,500 individual plants in April, 206 in June and 100 in July.

R. S. A.

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